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Environmental interpretation of the atrypid shell beds from the Middle to Upper Devonian boundary of the Holy Cross Mts and Cracow Upland

ABSTRACT: As indicated by a comparative analysis of atrypid shell beds yielded by stromatoporoid-coral limestones at the Middle to Upper Devonian boundary at Chęciny (Holy Cross Mts) and Dębnik (Cracow Upland), the atrypid *Desquamatia* was widely tolerant of environmental conditions. It formed a pioneer assocation able to colonize intershoal, poorly aerated habitats (Dębnik), as well as those periodically influenced by restricted logoons in conditions of fluctuating (?lowering) salinity (Chęciny). The shell size and morphology of *Desquamatia* is variable depending upon environmental variation related especially to the environmental stress and toxicity being higher at Dębnik than at Chęciny. Atrypid shell beds produced by monotypic population of *Desquamatia* are characteristic of Givetian to Frasnian transitional beds in Poland, West Europe, and the United States. In the systematic part of the paper the atrypid *Desquamatia (Seratrypa) globosa* (Gürich) and the associated cyrtospiriferid *Uchtospirifer nalivkini* Lyashenko are described.

INTRODUCTION

The lower part of stromatoporoid-coral limestones of the Holy Cross Mts and the Cracow Upland, traditionally attributed to the Middle Devonian (for review *see* Kaźmierczak 1971a) but actually representative of the Middle to Upper Devonian boundary sequence (Racki 1980; *see also* Kaźmierczak 1971a, Kaźmierczak *in* Biernat & Baliński 1973, Baliński 1979), often contain brachiopods, first of all atrypids (Zeuschner 1868; Zaręczny 1889; Gürich 1896, 1903; Siemiradzki 1909; Sobolev 1909). The previous workers distinguished three widely, but nevertheless variously meant atrypid species, namely *Atrypa reticularis* (Linnaeus), *A. desquamata* Sowerby, and *A. aspera* Schlotheim. Since that time, the atrypid taxonomy has been much refined (Alekseeva 1962; Struve 1966; Copper 1966b, 1967b, 1973, 1978) and a lot of modern paleoecologic work has been done on the atrypids (Copper 1966a, 1967a; Watkins 1975; Worsley & Broadhurst 1975; Smith 1976). The atrypids from the stromatoporoid-coral limestones of Poland are, nonetheless, most commonly attributed (Siedlecki 1954, Kotański 1959, Bieda 1966; see also Filonowicz 1973) to

A. reticularis, even though that species seems to be confined to the Silurian (Struve 1966, Copper 1973).

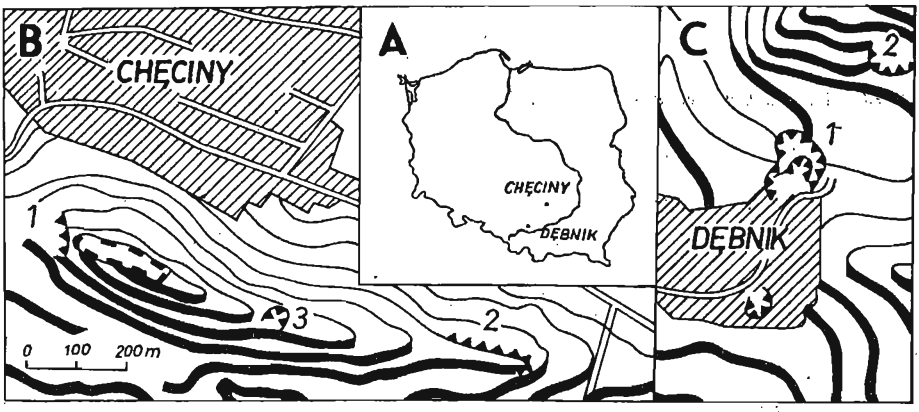

Fig. 1. Location of the investigated sections in Poland (**A**), and of the studied outcrops (numbered *1*, *2*, *3*) along the Zamkowa Hill at Chęciny (**B**), and in the Dębnik area (**C**; scale as in **B**: *1* Main Carmelite Quarry; *2* quarry above the Rokiczany ravine)

The present paper is aimed to reconsider the atrypids from the stromatoporoid-coral limestones of Poland from both systematic and ecologic standpoint, basing upon a comparative analysis of atrypid shell beds exposed at Chęciny in the Holy Cross Mts and at Dębnik in the Cracow Upland, almost a hundred kilometers in distance from one locality the other (Text-fig. 1*A*).

The paleoecologic part of the paper is by G. Racki, and the systematic part is by A. Baliński.

The investigated paleontological collection is housed at he Institute of Paleobiology of the Polish Academy of Sciences at Warsaw, kept under the catalogue number *ZPAL Bp. XXVII.*

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METHODS OF ECOLOGIC INVESTIGATION

Selected atrypid shell beds from Chęciny and Dębnik have been mapped (Text-figs 4—6 and 7) and presented in a synthetic form (Text-figs 3*B* and 6*B*).

Furthermore, microfacies and unsoluble in acetate acid residuum of the rocks were analysed. Rock constituents were investigated by point countaing with

Fox & Brown's (1965) modification of the grain-bulk rule. Folk's (1962) terminology has generally been accepted, with peloid/intraclast boundary arbitrarily set at the grain size of 0.12 mm, and 250 points per thin section were analysed on the average and hence, the standard error of estimates should not exceed 6% (*cf.* Flügel 1978, Fig. 24). However, this error may be much greater in the case of diagenetically changed limestones from Chęciny. In addition, granulometric parameters were estimated after 100 points per thin section on the average, biotic components were analysed by Carozzi's technique (*cf.* Carss & Carozzi 1965, Roche & Carozzi 1970), and petrographic fossil diversity (*sensu* Smosna & Warshauer 1978) was studied.

Table 1

Microscopic characteristics of the rock			Genetic interpretation				Representative rock types[1]
Allochems, %	Micrite/sparite ratio	Sorting	Winnowing[1]	Environmental energy[2]	Benthic biotope[3] /substrate/	Hydrodynamic category[1]	
<1	only micrite	indeterminate	non-washed	quiet water	muddy bottom	I	micrite, dismicrite
1-10	—— " ——	—— " ——	—— " ——	—— " ——	—— " ——	II	fossiliferous micrite, etc.
10-50	>> 1.5	—— " ——	—— " ——	—— " ——	—— " ——	III	sparse biomicrite, pelmicrite, etc.
>50	> 1.5	—— " ——	—— " ——	slightly agitated water	—— " ——	IV	packed biomicrite, pelmicrite, etc.
	1.5-0.5	unsorted	partly washed	—— " ——	muddy bottom → → sandy bottom	V	poorly washed biosparite, intrasparite, etc.
	<0.5	—— " ——	washed, but unsorted	moderately agitated water	sandy bottom	VI	unsorted biosparite, intrasparite, etc.
	—— " ——	moderately to well-sorted	washed, sorted	—— " ——	—— " ——	VII	sorted biosparite, intrasparite, etc.

Hydrodynamic categories assumed for environmental interpretation of limestones, based on textural spectrum of Folk (1962) and conception of energy index (Plumley & *al.* 1962; modified by Čatalov 1972)

In captions: 1 — after Folk (1962); 2 — after Plumely & *al.* (1962), Catalov (1972), and Flügel (1978); 3 — after Čatalov (1972)

The obtained data have been arranged to present time-trends of lithologic and paleontologic variables (Text-figs 3*A* and 6*A*). The former variables were used to recognize the environmental energy level (Table 1), while the latter to estimate other environmental parameters. To this end, paleontologic characteristics of the investigated rocks were analysed in terms of ecologic groups (*cf.* Salin 1972).

DESCRIPTION OF ATRYPID SHELL BEDS

CHĘCINY

The considered atrypid shell bed occurs in the western quarry in the Zamkowa (Castle) Hill at Chęciny (exposure *1* in Text-fig. *1B*), within a 50 m thick series of grey-colored, fine-grained, organodetrital limestones (Text-fig. 2 and Pl. 1, Fig. 1). The age attribution of that

series is disputable (*see* Kaźmierczak 1971a, b; Szulczewski 1979) but the conodonts found herein (*Polygnathus pollocki* Druce, *P. pennatus* Hinde, and *P. dubius* Hinde) indicate that it is not older than the Upper hermanni-cristatus Zone (*see* Racki 1980).

The set *F* of the series under discussion is distinctly tripartite owing to recurrence of characteristic lithologies. The subsets (*F-I* to *F-III*) contain each an atrypid shell bed in the middle (Text-figs 2, 3A; Pl. 1). The greatest shell accumulation certainly is the lowest one (shell bed *F-I* in Text-fig. 3*A*; Pl. 1), commonly called a coquina (*e.g.* Szulczewski 1979); however, the latter term is applicable to some parts of the shell bed only (Text-figs 3*B* and 4) because the brachiopod shells account for less than 10% of the entire bed.

The bed F-I consists of a fine-grained calcarenitic, rich biopelmicrite (Pl. 3, Fig. 1; Pl. 4, Figs 2—3; Pl. 6, Fig. 4; Pl. 7, Figs 1 and 3—4), more or less nodular in structure which is reflected by a structural variation in a single thin section (*cf.* Hopkins 1977). The nodules include rock fragments covered, often entirely, with a shell (*cf.* Narkiewicz-1978a, b) and atrypid shells deformed dependingly upon their position in the rock (*cf.* Fergusson 1962).

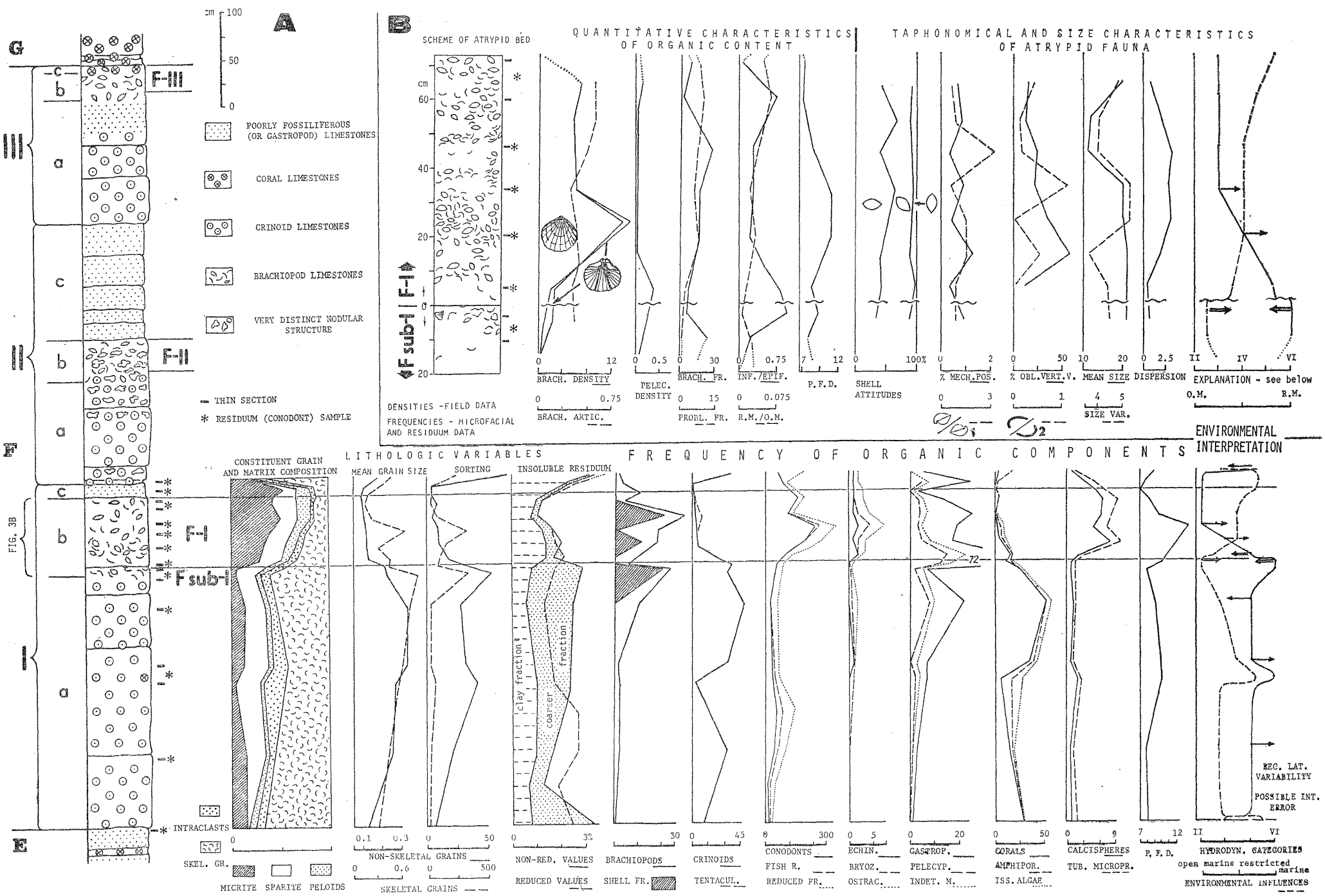
The atrypid species *Desquamatia (Seratrypa) globosa* (Gürich) accounts for more than 90% of the macrofauna. It is associated with a few specimens of *Uchtospirifer nalivkini* Lyashenko, locally abundant dendroidal stromatoporoids, pelecypods (mostly at the base of the shell bed), gastropods (chiefly *Pleurotomaria* and *Loxonema*), and fragmented crinoids (genera *Stenocrinus, Anthinocrinus* and *Kasachstanocrinus*; identified by Dr. E. Głuchowski). As evidence by thin sections, the skeletal components are abundant and diverse (*P.F.D.* = 8—12). They include echinoid spines, fragmented bryozoans (Pl. 7, Fig. 3) and corals, ornamen-

Explanation of Text-fig. 3

Taphonomic and shell size parameters were determined for a belt of 10 cm; density was calculated per 100 cm2. In estimations taken for granted, 2 valves equal 1 shell. Mechanic positions (*cf.* Ager 1963) were defined as oblique and vertical shell orientations with foramen upward. Articulation expresses proportion of articulated shells. "Shell size" refers to the size of shell section on the mapped area (*see* Text-fig. 11). Dispersion, "shell size" and grain size variabilities were calculated as a standard error; mean size equals medial size. In each thin section, the frequency of organic components was counted over a surface area of 100 mm² (larger grains) or as average of 5 counts of 1.44 mm² (microbiota). In case of occurrences of whole shells, it was assumed that 1 shell equals 10 fragments of valves. Frequency of microfossils was determined for 2 general groups: calcispheres (*cf.* Kaźmierczak 1976), problematic single-chambered foraminifera (mainly *Parathurammina, Bisphaera, Irregularina*), and tubular microproblematics (mainly *Magnella, Uraloporella*). Residuum contents, frequency of conodonts and fish remains were counted as absolute (non-reduced) values and with regard to contribution of skeletal grains (reduced values).

Abbreviations: *SKEL. GR.* — skeletal grains, *FR.* — frequency, *INDET. M.* — indeterminate mollusks, *ISS. ALGAE* — algae of the type *Issinella, TUB. MICROPR.* — tubular microproblematics, *P. F. D.* — petrographic fossils diversity, *INF./EPIF.* — total values of frequency of infauna (= pelecypods) and epifauna (mainly brachiopods, crinoids and gastropods), *R.M./O.M.* — total values of frequency of restricted-marine (calcispheres, other microproblematics, amphiporoids; *cf.* Kaźmierczak 1976, Vachard & Tellez-Giron 1978, Riding 1979) and open-marine fossils (echinoderms, brachiopods, bryozoans, tentaculitids, conodonts, fishes), *% MECH. POS.* — proportion of mechanic positions (for shells), *% OBL. VERT. V.* — proportion of oblique and vertical orientations (for valves)

Symbols: *1* alternative horizontal shell orientations ratio, *2* alternative horizontal valve orientations ratio; for hydrodynamic categories see Table 1



Results of microfacies investigations of the set *F* exposed in the Zamkowa Hill at Chęciny (**A**), and scheme of the atrypid shell bed *F-I* from that section (**B**)

ted and smooth ostracodes, calcareous algae with tubular thalli resembling *Issinella* (see Maksimova 1977), abundant volvocean calcispheres (most commonly at the *"Vicinesphaera" and "Archaeosphaera-Pachyspherina"* preservation stages of Kaźmierczak 1976), tubular microproblematics (Pl. 7, Fig. 4) resembling *Magnella* (see Neumann & *al.* 1975) reinterpreted recently as fragmented spiriferid microspines (Vachard & Tellez-Giron 1978), some other microproblematics (*Uraloporella*, radiospheroidal calcispheres, and supposed single-chambered foraminifera, mostly *Parathurammina*). There are also relatively common conodonts (up to 300 specimens per kilogram).

The atrypid shell bed *F-I* is underlain by crinoid limestones (*F-Ia* in Text-fig. 3*A*) with infrequent gastropods, fragmented pelecypods and corals, and a thin layer with branched rugose corals (*Disphyllum*) and a few atrypids. As evidenced by thin sections, the rock contains echinoid spines, ostracodes, amphiporoids, and *Issinella*-like algae (Pl. 5, Fig. 2). Furthermore, some micrite grains show a structure suggestive of their algal origin (*cf.* Wolf 1965, Maksimova 1977). The rock displays indistinct swirls and a hardly discernible nodular structure (Pl. 4, Fig. 1).

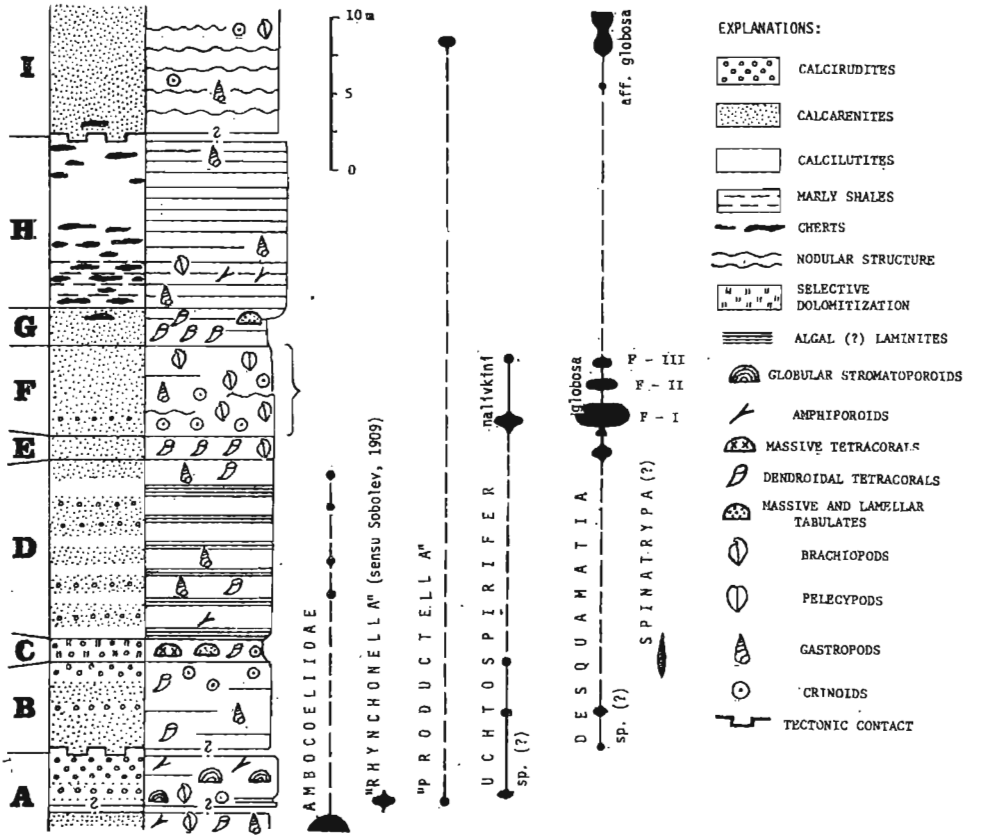


Fig. 2. Section of the western quarry in the Zamkowa Hill at Chęciny (*partly after:* Kaźmierczak 1971a, Szulczewski 1979) showing the sequence of brachiopods; note the frequent occurrence of atrypids and cyrtospiriferids (? commensal association of Copper 1966a); *F-I*, *F-II*, *F-III* atrypid shell beds

There is a considerable neomorphism and some peloids could develop due to aggradation of calcareous algal fragments that originally made up their coating (*cf.* Maksimova 1977). This may indicate that the initial proportion of micrite was higher than it is at present. On the other hand, there is evidence for both pre-compactional and post-compactional cement, *viz.* dog-tooth spar (*cf.* Schneider 1977) and druse mosaic, respectively, as well as large amounts of sparite filling up primarily voids (Pl. 5, Fig. 4). There are also some accumulations of peletal micrite under bioclasts (Pl. 5, Fig. 2) and within shells. One may therefore conclude that the considered crinoid limestones are partly washed, coarse-grained intrabiosparites.

The crinoid limestones are separated from the atrypid shell bed *F-I* by a thin, brachiopod-bearing bed (*F sub-I* in Text-fig. 3A). There is some variation in faunal composition and preservation, as well as in microfacies. Where fragmented *Uchtospirifer nalivkini* prevails, the microfacies resembles the underlying crinoid limestones (see Pl. 4, Fig. 1; Pl. 5, Figs 1 and 4). Elsewhere, *Desquamatia*

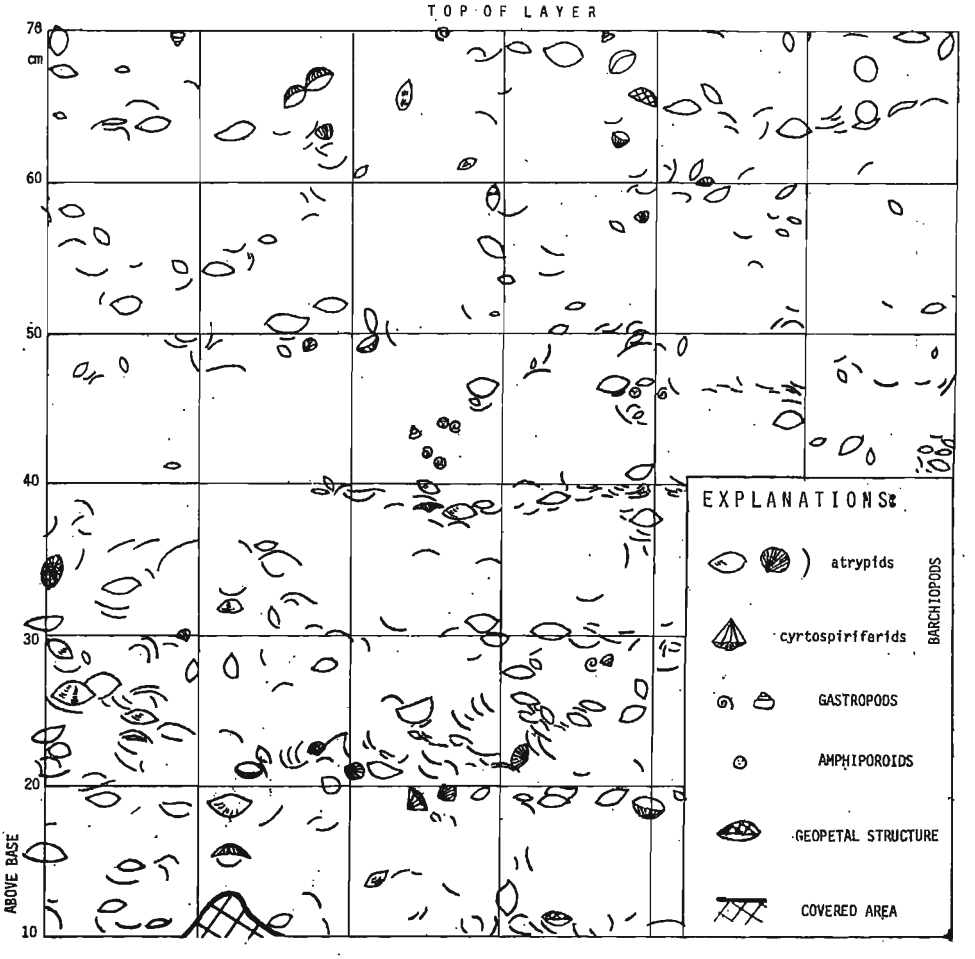


Fig. 4. Distribution of fauna in the atrypid shell bed *F-I* at Chęciny; note irregular arrangement of fossils and levels of strongly crushed valves

obosa considerably contributes to the fossil assemblage, the fossils are better preserved, and the microfacies resembles the atrypid shell bed. The occurrence of isolated valves of the pelecypods *Pterinopecten* and *Jahnia* is notable. The contact of this layer with the atrypid shell bed is hardly discernible in places and irregular, suggestive of its origin due to a pressure-solution process. If so, it may reflect a diastem only in part.

The atrypid shell bed *F-I* is overlain by a biopelmicritic bed resembling in microfacies the top of the shell bed itself (*see* Pl. 4, Fig. 4), rich in microproblematics and ostracodes, but without any macrofauna except for gastropods and crinoids.

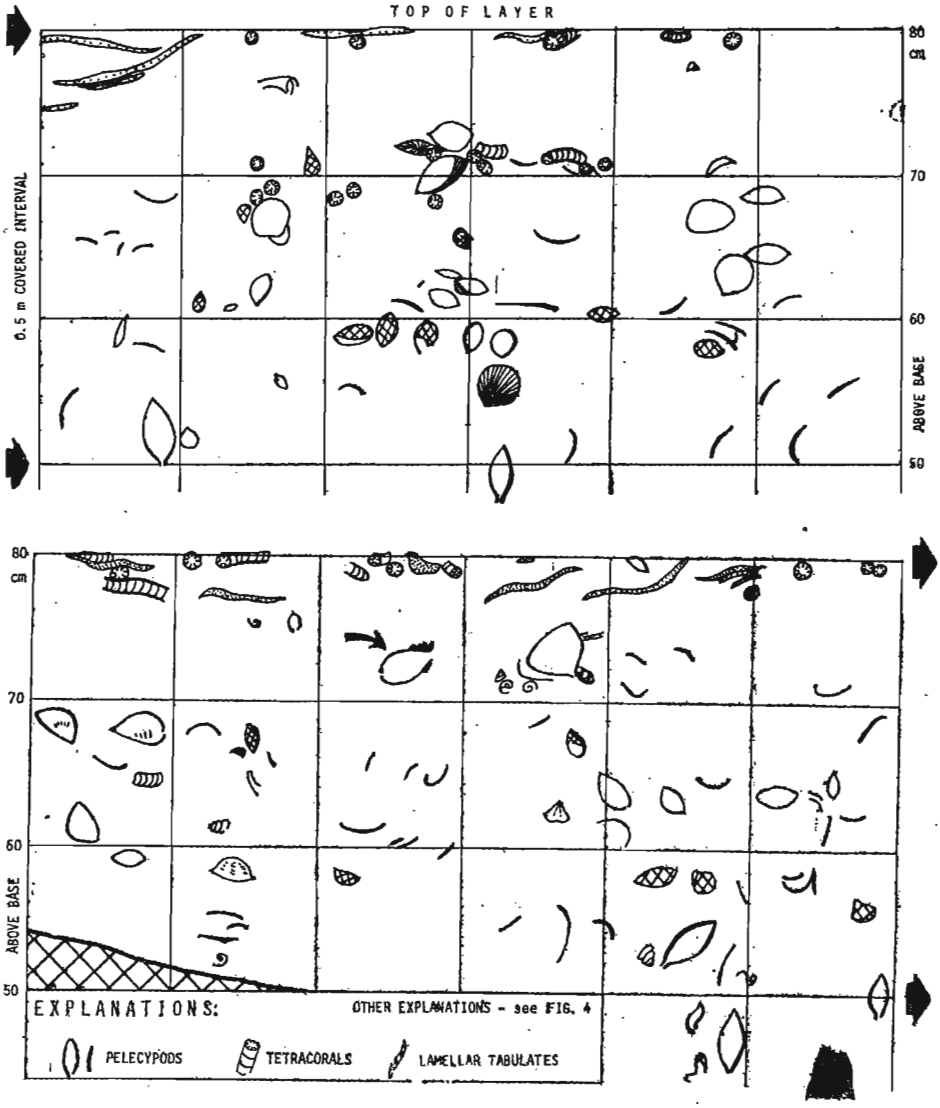


Fig. 5. Distribution of fauna in the atrypid shell bed *F-III* at Chęciny; note a frilled atrypid shell (*arrowed*)

The atrypid shell bed *F-I*, thick up to 1 m, is exposed also in the eastern part of the Zamkowa Hill (exposure *3* in Fig. 1*B*). The fauna is there considerably richer in *Uchtospirifer nalivkini*; more common and diverse are also the pelecypods (*Pterinopecten, Carydium, Actinopteria, Mytilarca, Nuculoidea*) and gastropods (*Pleurotomaria, Euomphalus, Bellerophon*) and corals. The enclosing rock (Pl. 3, Fig. 2) closely resembles that found in the western quarry, except for being more bioturbated (Pl. 7, Fig. 2) and with somewhat less diverse skeletal components (*P.F.D.* = 6—9). However, the atrypid shell bed is underlain partly by coral limestones and/or non-fossiliferous calcarenites instead of crinoid limestones.

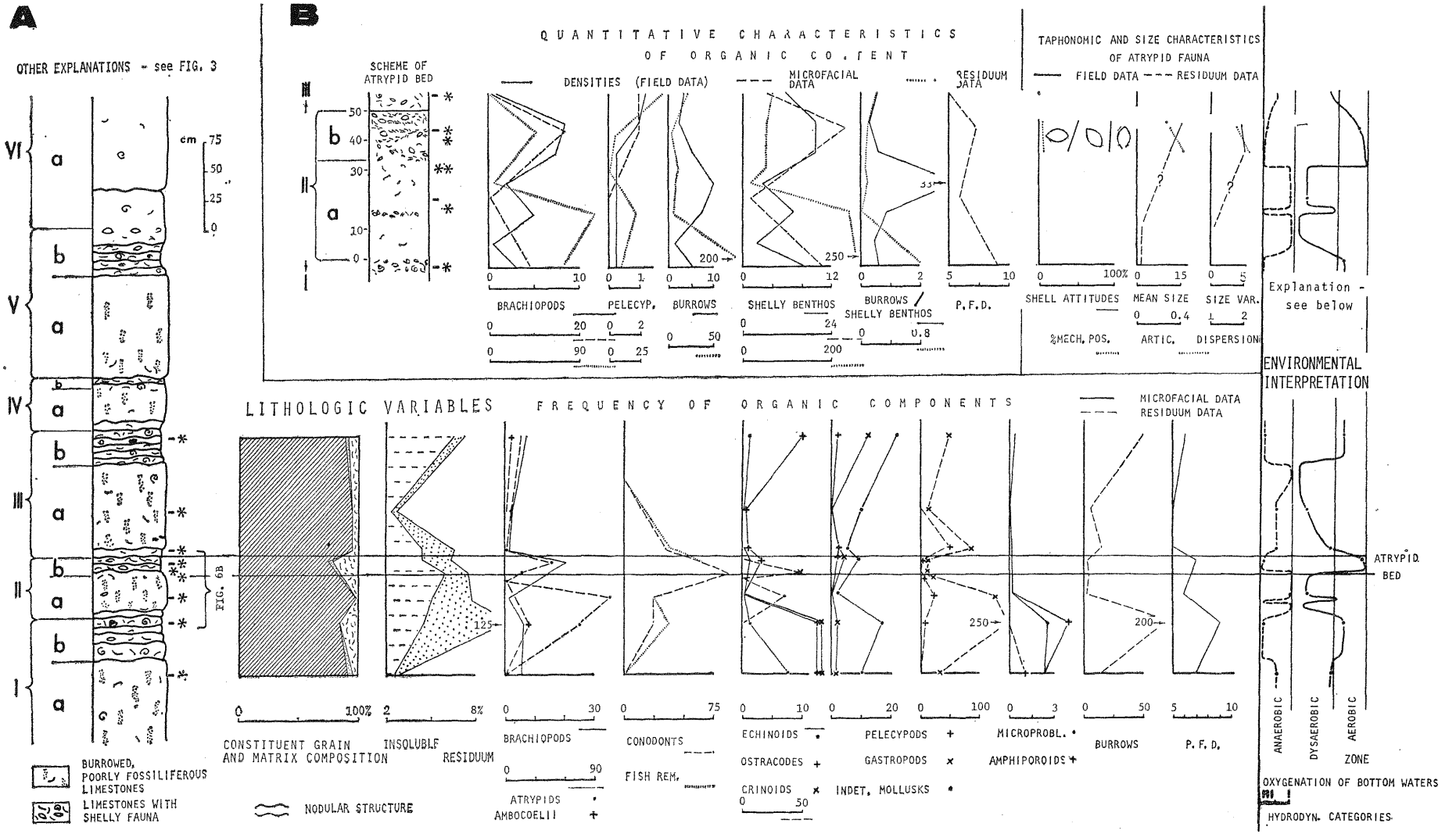
As observed in the western quarry, the subsets *F-II* and *F-III* resemble the above discussed *F-I* (Text-fig. 3*A* and Table 2; Pl. 6, Figs 1—2), except for the crinoid limestones (*see* Pl. 6, Fig. 3) and the atrypid shell beds decreasing in thickness, and the atrypids being preceded by mollusks, mostly large-sized pelecypods (*Pterinopecten* and *Edmondia* among others), often in life position (Text-fig. 5). At the top of the shell bed *F-III* the atrypids become replaced with corals which reflects a transition to the coral-limestone set *G* (Text-figs 2, 3*A*).

Table 2

Parameter \ Atrypid shell bed		Zamkowa Hill at Chęciny				Dębnik
		Fsub-I	F-I	F-II	F-III	
Thickness of atrypid level /in cm/		5-15	65	40	25	15-20
Mapped area /in cm^2/		3300	6000	3600	5000	1500
Contribution of atrypid level to total thickness of bed, %		up to 50	90	60	30	15
Mean density /in specimens per 100 cm^2/		2.5 /a-0.5/	7.7	5.1	1.3	7/?/
Articulation		0.27 /a-0.52/	0.50	0.49	0.73	0.30
Disperaion		2.2	4.2	3.0	0.8	2.0
Mean shell size	field data	20	18	23	30	15
	collection	?	19.5	24.0	30.9	17.2
Size variability		4.2	4.9	4.9	4.2	2.7
Positions, %	horizontal	?	49.5	40	43	46.8
	oblique	?	45.2	56	46	48.9
	mechanic	?	9	8.5	8.1	6.4
Alternative horizontal shell orientation ratio		?	1.15	0.83	1.10	0.56

Quantitative characteristics of the atrypid shell beds at Chęciny and Dębnik; note increase of the shell size from bed *F-I* to *F-III*, and differences between atrypid fauna from the both localities (*see* also Table 3); marked with α are data only for atrypids in bed *Fsub-I*

The atrypids occur also at the top of the set *I* (Text-fig. 2 and Pl. 1, Fig. 1) That shell bed is best exposed in a pit in the central part of the Zamkowa Hill (exposure *2 in* Text-fig. 1*B*) where the atrypids, *Desquamatia* aff. *globosa*, locally occur in coquina-like accumulations. The atrypids are much less frequent in the sets *B* and *E* (less than 1 specimen per 100 cm^2) where they occur with mollusks and precede coral-bearing layers.



Results of microfacies and residuum (for silicified fauna) investigations of the atrypid-bearing section exposed in the Main Carmelite Quarry at Dębnik (**A**), and scheme of the atrypid shell bed (= set *II*) from that section (**B**)

DĘBNIK

The atrypid shell bed occurs in the Main Carmelite Quarry (exposure *1* in Text-fig. 1C; Pl. 2, Fig. 1), in the upper part of a 35 m thick series of dark-colored, pyritiferous and with up to 6% of clay matter, generally poor in fauna calcilutites (*cf.* Baliński 1979, Łaptaś 1979). That series traditionally was assigned to the Givetian but the conodont assemblage indicates that it is not older than the Upper hermanni-cristatus Zone (*see* Baliński 1979).

There are some sedimentary lithologic sets (*I* to *V*) in the upper part of the series, somewhat indistinct from one another due to irregular development of nodular layers (Text-fig. 6*A*). The lower part of a set (Text-fig. 7*c*) normally is represented by massive bioturbated micrites with more or less frequent vertical or oblique burrows, variable in cross section (2—5 mm in diameter), sometimes branching, filled up with coarser-grained sediment enriched in pellets and pseudointraclasts (*cf.* Flügel 1978, Table 13). Irregular streaks of intrarudite occur here and there. The fauna is very poor, composed of minute gastropods and a few pelecypods.

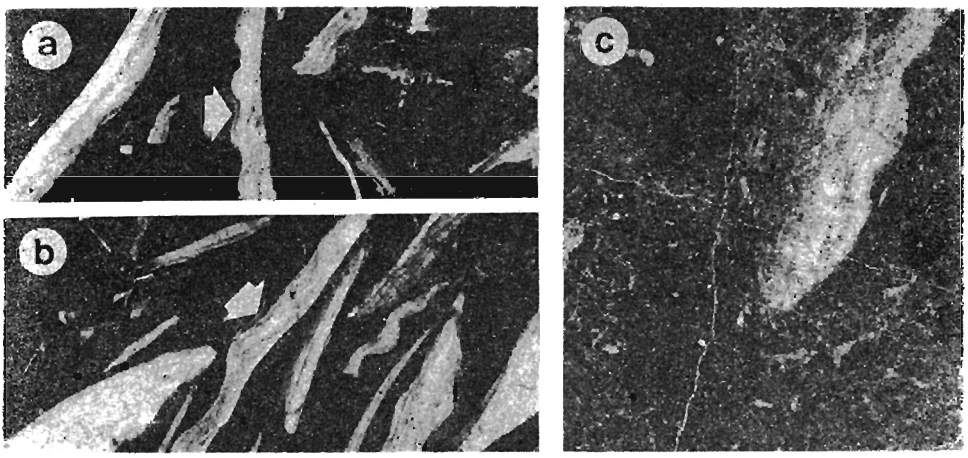


Fig. 7. Typical microfacies of the Dębnik limestone

a-b — Atrypid biomicrite (arrowed are fragments of frills); atrypid shell bed, quarry above the Rokiczany ravine; × 20

c — Bioturbated micrite (regular outline of the burrow suggests peristaltic motion of an unknown burrower); unit *IIa*, Main Carmelite Quarry; × 15

The upper part of a set (*see* Text-fig. 7a-b) normally is represented by biomicrites nodular in structure (*cf.* Narkiewicz 1978a, b), with fairly abundant although fragmented and poorly diversified fauna (Text-fig. 8). There are some coquinas consisting of variable proportions of gastropods (*Murchisonia, Glyptospira, Loxonema, Straparollus*), pelecypods (*Lyriopecten, ?Conocardium, Macrodus*), and brachiopods (atrypids with minor amounts of ambocoelids). As evidenced by thin sections, the fossil assemblage includes also ostracodes, echinoid spines, amphiporoids, problematic calcispheres, a few kamenids and supposed renalcids. The

maximum frequency of conodonts also is in the coquinas. Silification of fauna is notable and some systems of branching striated burrows (Text-fig. 7c) have been recorded from residuum which resemble the "Würmröhre" described by Wiencierz (1973) from Lower Jurassic deposits.

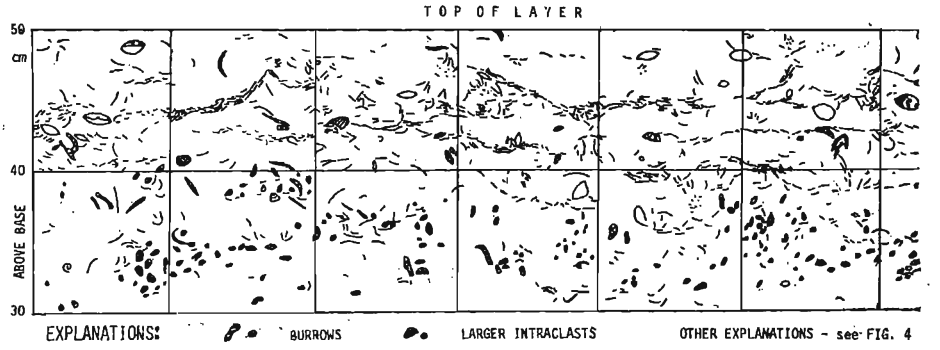


Fig. 8. Distribution of fauna in the atrypid shell bed at Dębnik; note the well developed levels of crushed valves along the solution partings, as well as bioturbations in the lowermost part of bed 1

The most important atrypid shell bed (Pl. 2, Fig. 2) in that exposure (it is recognizable also 200 m to the north, in a quarry above the Rokiczany Dół ravine; exposure *2* in Text-fig. 1C) is in the set II and corresponds to the *Desquamatia (Seratrypa) oneidensis* Range Zone of Baliński (1979; unit *IIb* in Text-fig. 6A in the present paper). The atrypids are associated with minute gastropods, crinoid trochites, and pelecypods, the latter increasing in number above. The atrypid shells bear an epifauna (spirorbids). There are some local accumulations of juvenile *Desquamatia oneidensis* in the lower part of the set (Pl. 9, Fig. 8).

The atrypids are very small-sized (5—10 mm at the maximum) and infrequent in the remaining coquinas at Dębnik. However, an accumulation (*ca.* 3 specimens per 100 cm²) of large-sized atrypids *Desquamatia* sp. occurs also in the set *V*.

PALEOENVIRONMENTAL INTERPRETATION

Reworking of the investigated atrypid shell beds is indicated by shell disarticulation and fragmentation and by fossil orientation (*see* Text-fig. 9). Nevertheless, the evidence for destruction of fossils often coincides with evidence for consierable compaction and pressure solution (Text-figs 4 and 8; Pl. 4, Figs 1—2), or for biogenic reworking (Text-fig. 7c; Pl. 3, Fig. 2; Pl. 5, Fig. 2; Pl. 6, Fig. 2; and Pl. 7, Fig. 2). On the other hand, there are several reasons to claim that post-mortem transportation and sorting of fossils was insignificant. Generally, the enclosing rocks (Text-figs 3 and 6) are representative of the hydrodynamical categories *III* and *IV*, or quiet to slightly agitated-water environoments (Table 1). There is a large proportion of articulated shells (Table 2), often preserved, even if fragmented, with fragile morphological elements, as *e.g.* the frills (Pl. 4, Fig. 2; Pl. 6, Fig. 1; and Pl. 7, Fig. 4). The orientation of

shells is correlated with their size (Text-fig. 9*A*), in consistency with ontogenetic changes in presumed atrypid life position, as well as there is no correlation of abundance of mechanic positions with shell size (Text-fig. 9*B*). The fauna is irregularly distributed, often in nests (Text--figs 4—5), and the non-brachiopod macrofauna commonly is in life position. Thus, one may conclude that post-mortem transformations of the fossil assemblage did not significantly changed its structure, except possibly for some impoverishment in juvenile shells. Exception is mainly the brachiopod-bearing bed *F sub-I* at Chęciny (*see* Text-fig. 3) built up by biointrasparites representative of the hydrodynamical category *VI*.

The considered atrypid shell beds are therefore regarded as ecologically controlled brachiopod biostromes (*sensu* Aigner & *al.* 1978; *see also*

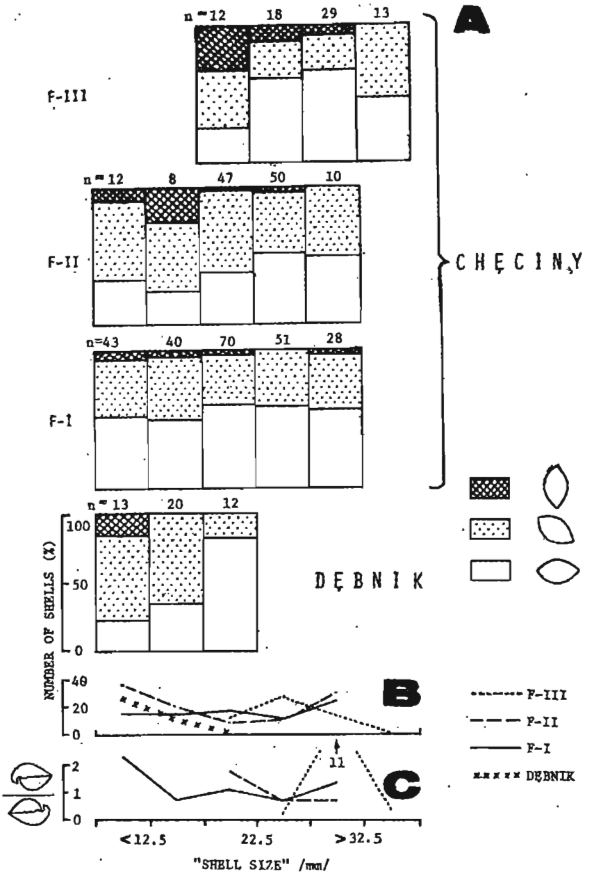


Fig. 9. Shell orientation in the investigated atrypid shell beds

A — Shell orientation in different clases of "size"; note many small shells preserved in non--horizontal position, what suggests changes in mode of life during ontogenesis (*cf.* Worsley & Broadhurst 1975)

B — Relative abundance of mechanic positions in different classes of "shell size"

C — Alternative horizontal orientation ratio in different classes of "shell size"

Wallace 1969). Their recurrence and constant position in lithological sequence permits their recognition for a distinct ecologic unit which is here designated by the term *assemblage* to avoid terminological confusion concerning the use of the term community in paleoecology (*cf.* Watkins & *al.* 1973, Ziegler 1974, Boucot 1975, Kauffman & Scott 1976).

As judged after the microfacies, taphonomic data, and general faunal adaptation (*e.g.* the prevalence of high-spired gastropods; *cf.* Peel 1978), the atrypid shell beds developed under conditions of quite to periodically slightly agitated water. The microfacies succession at Chęciny (Text-fig. 3B; compare Pl. 5, Fig. 2 and Pl. 7, Fig. 1) clearly shows that the hydrodynamic energy level decreases upwards in the set F-I. In Heckel's (1972) terms, this is a transition from abraded calcarenites through whole-shell calcarenites and almost to calcilutites. This transition must reflect a change in substrate nature for benthic animals. The brachiopod accumulations developed, indeed, on substrates intermediate in nature between crinoid sands and soft muds, namely on fine-grained sediments with variable proportions of calcareous mud and skeletal and non-skeletal grains. The peloidal nature of the calcareous mud may be partly due to the brachiopod life activities, *viz.* their rejection mechanisms (Rudwick 1970). The occurrence of large-sized, considerably biconvex atrypid shells indicates a compact substrate (Walker 1974, Faber & *al.* 1977) which could be effected by early cementation. This is, indeed, corroborated by some evidence for the neospar having largely developed from primary sparite matrix, *e.g.* aragonitic cement, as proposed by Beales (1965) for peloidal limestones; and for the nodular structure having developed by at least a selective early cementation (*cf.* Hopkins 1977, Narkiewicz 1978a; *see also* Kaźmierczak & Goldring 1978). In Dębnik this is indicated by distinct boundaries of burrows (Text-fig. 7c).

In turn, depositional environment of the atrypid shell bed of Dębnik could temporarily be stagnant (*cf.* Łaptaś 1979), and the substrate was soft and supposedly unstable due to infaunal activities (*cf.* Rhoads & Young 1970).

The bottom-sediment resusponsion by infauna, and consequently the water turbidity, could be high at Dębnik. It was increasing upwards a set at Chęciny, as both the proportion of calcareous mud and the bioturbation density increase upwards. The sedimentation rate, however, seems to have been changing in opposite direction. Its variability may partly account for the observed variation in distribution and preservation of fossils within the atrypid shell beds (*cf.* Bretsky & *al.* 1977, Fürsich 1978, Mundlos 1978).

The diverse calcifying macrobenthic assemblage and the presence of iron oxides in residuum indicate that the atrypid shell beds of Chęciny developed in well aerated habitats. The commonness of pyrite and pyritization phenomena, almost black color of the rock, and rather poor and small-sized calcifying macrofauna associated with a rich ichnocoenose indicate that the bottom habitat was, to the contrary, poorly oxygenated at Dębnik (dysaerobic zone of Rhoads & Morse 1971; *see also* Byers 1979).

The investigated atrypid shell beds are highly dominated by fossils generally conceived of as indicative of normal salinity.

At Chęciny, however, there are also fossils, mostly microproblematics and amphiporoids, reported most commonly from restricted marine environments, first of all so-called back-reef lagoons (facies 11—12D of Wilsons 1975). They often show much evidence for redeposition and sometimes they make part of intra-

lasts (Pl. 6, Fig. 4 and Pl. 7, Figs 2—4); this is especially the case with poorly preserved volvocean calcispheres (*sensu* Kaźmieczak 1976) that could easily be isolated from intraclasts during a transportation (*cf.* Carss & Carozzi 1965). This can be most plausibly interpreted as due to supply of bioclacts from adjacent restricted lagoons to a generally normal marine environment (*see* Willson 1975 — facies 10D, Kaźmierczak 1976, Kaźmierczak & Goldring 1978). Consequently, the salinity may have been fluctuated and temporarily decreased, too (*cf. also* Linsley 1973). In fact, the abundance of phyllopods and charophytes is suggestive of a possible decreased salinity in some depositional environments of the stromatoporoid-coral limestones from the Holy Cross Mts (Baliński 1973, Racki & Racka 1981). The ability of normal marine macrobenthos to persist under conditions of an influx of water from restricted lagoons can be explained by a density stratification of water derived from diverse environments. It was, indeed, observed by Behrens (1965) that off the Monkey River mouth, Cetnral America, the nearbottom water layers maintain normal salinity even though the surficial water is brackish and highly turbid. The salinity fluctuations (accompanied also by temperature changes; *cf.* Linsley 1973, Heckel & Witzke 1979) seem to have been the greatest at the time the crinoid limestones were deposited (there are both amphiporoid- and coral-bearing intercalations; Text-fig. 3A) but generally the salinity is thought to have been decreasing upwards a set (Text-fig. 13). In fact, this could be the ultimate limiting factor of the atrypid assemblage proliferation, because the topmost layers of a set often resemble in lithology beck-reef facies (*cf.* Wilson 1967, Roche & Carozzi 1970, Krebs 1974, Neumann & *al* 1975).

The investigated atrypid shell beds developed in a shallow offshore (*cf.* Kaźmierczak 1971a, b; Szulczewski 1971; Narkiewicz 1978b) on the vast tropical shelf (House 1975, Heckel & Witzke 1979). The atrypid shell beds of Chęciny are both preceded and succeeded in the facies sequence by coral limestones. Devonian brachiopods are generally thought to have settled somewhat deeper habitats than those occupied by (after Lecompte 1958) corals, the latter environments being estimated for some 20 m in depth (Embry & Klovan 1972, Errera & Mamet 1973, Read 1973, *see also* Copper 1966a).

As judged after the euxinic conditions (*cf.* Byers 1977) and the scarcity of algae and grain micritization, the Dębnik basin was deeper than the Chęciny one (*cf.* Łaptaś 1979). Its stagnation may have been due to a barrier hampering the lateral exchange of water. In turn, the Zamkowa Hill area at Chęciny is unique in that part of the Holy Cross Mts in the scarcity of stromatoporoid biostromes and the prevalence of fine-grained organodetrital deposits in the considered stratigraphic interval (*see* Kaźmierczak 1971a, b; Filonowicz 1973). One may therefore claim that this was a sheltered intershoal area (Text-fig. 10) surrounded, at least in the north and west, by irregular, vast bank areas with prolific growth of stromatoporoids and corals, and blue-green algal mats (*cf.* Kaźmierczak 1971b). The depositional environment seems thus to have been analogous to that inferred for some limestones of the Givetian Traverse Group, Michigan (Roche & Carozzi 1970; see also Tyler 1969,

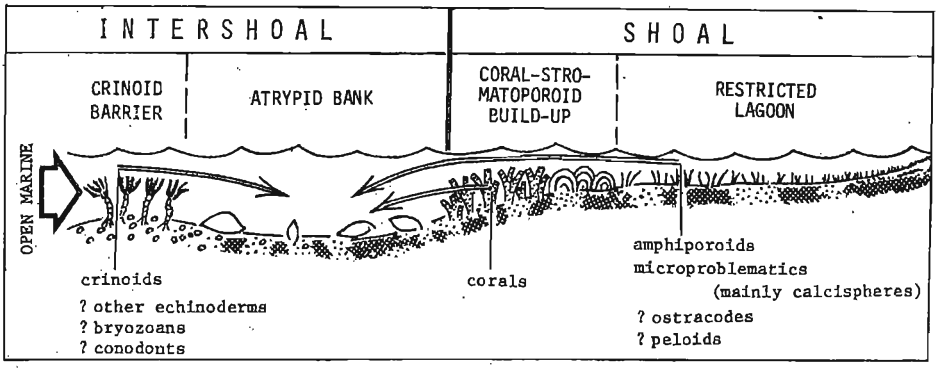


Fig. 10. Facies pattern for the Chęciny limestone during development of the atrypid shell beds

Ehlers & Kesling 1970); this is, indeed, corroborated also by a similarity in the atrypid fauna (*see* Systematic part).

The repeated appearance of crinoid limestones and their constant relationship to an increase in environmnetal energy level are notable. Common and rapid replacements of low-energy wackestones with high-energy, cross-bedded packstones and grainstones have been described by Morrow (1978) from the Middle Devonian Dunedin Formation, Canada, and interpreted as migrations of high-energy shoals into more sheltered areas during storms (*see also* Krebs 1974). Similarly, Nowak & Carozzi (1972) referred to a discontinuous crinoidal bar grading into back-bar lagoon to explain the sedimentary patterns recorded in the Pennsylvanian to Permain Bird Spring Group in Nevada. Such an interpretation may hold true also in the presently discussed case, although the rate of changes in hydrodynamics certainly was lower than in the above cited cases.

AUTECOLOGY OF ATRYPIDS

The atrypid genus *Desquamatia* apparently was able to settle intershoal habitats, generally unfavorable for shelly fauna, especially ones adjacent to coral patches or banks (*cf.* Copper 1966a, b, 1967a). Its high adaptedness may have been partly due to the complexity and efficiency of the lophophore (*cf.* Fürsich & Hurst 1974), presumed high reproductive rate, and tolerance of fluctuations in salinity (*cf.* Ivanova 1962, Wilson 1967, Linsley 1973) and oxygen contents in the water; the latter characteristic may have been due to the spherical shell shape permitting among the others maintenance of relatively large quantities of water in the mantle cavity (*cf.* Faber & *al.* 1977).

As indicated by the size-frequency and convexity-frequency distributions (Text-figs 11—12; Table 3), the latter feature being indicative of atrypid ontogenetic maturity (*cf.* Watkins 1975 Worsley & Broadhurst 1975), the biotopes of particular atrypid shell beds were variable with respect to their suitability for the atrypids. Presumably, the most suitable biotope was coresponding to the shell bed *F-III* at Chęciny, the most quiet-water one and with the least densely packed shells. In fact, the atrypids from that shell bed are very large-sized (up to 40 mm) but nevertheless, they still did not achieve the gerontic stage. In general, the biotopes observed at Chęciny fall within the range of habitats commonly inferred for the environmental framework favorable for atrypid proliferation (*see* Copper 1966a, b 1978; Schumacher 1971; Linsley 1973; Boucot 1975; Watkins 1975; Worsley & Broadhurst 1975; Faber & *al.* 1977; Feldman 1980, Watkins & Aithie 1980). The stunted nature of the atrypids from Dębnik may be indicative of the subeuxinic biotope hav-

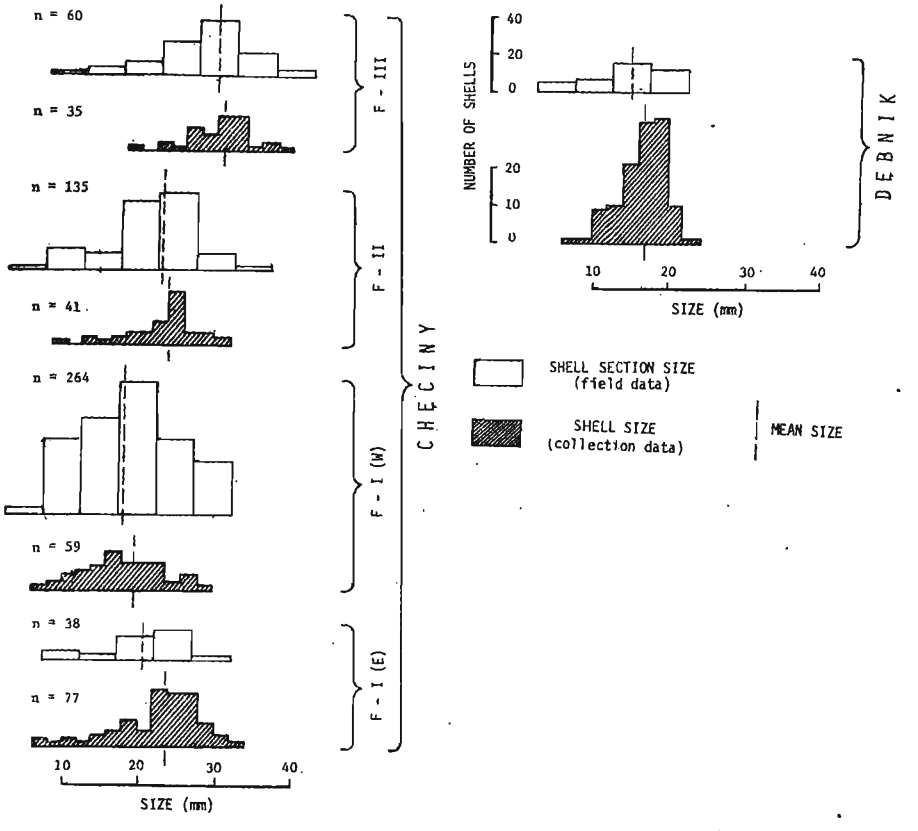


Fig. 11. Comparison of size-frequency distribution in different shell beds (*see* Text-fig. 3 for explanation); note a similarity of mean values in both groups of data; *F-I(W)* western quarry, *F-I(E)* eastern outcrops at Zamkowa Hill, Chęciny

ing been less suitable for those brachiopods (in fact, the genus *Spinatrypa* as well as *Desquamatia* seem to have prevailed in Middle Devonian stagnant basins; Copper 1966a), but it may also reflect an adaptation to life on small hard substrates (*cf.* Surlyk 1972).

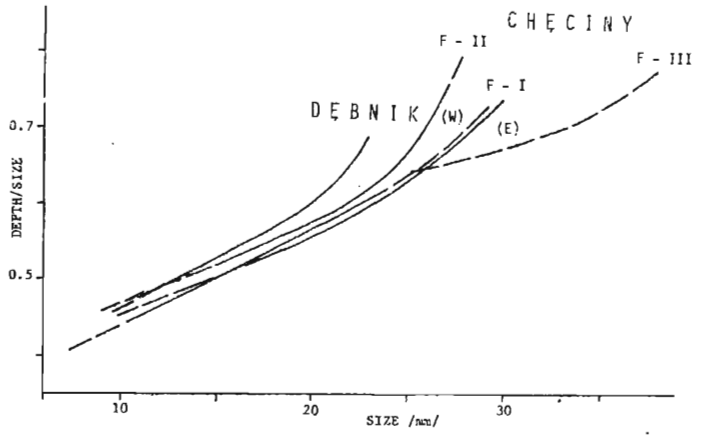


Fig. 12. Dependence of thickness index to shell size for the atrypid faunas from different shell beds (*see* also Text-fig. 18; and for explanations Text-fig. 11)

The significance of pedicle for orientation of atrypid brachiopods was decreasing in ontogeny (Ivanova 1962, Copper 1967a, Watkins 1975, Worsley & Broadhurst 1975). In fact, most adult atrypids from Chęciny were free-living. This is, however, not the case with those from Dębnik which show a biconvexity and a weakly curved beak (Baliński 1979) making an evidence for maintenance of an active pedicle even at the gerontic stage (*cf.* Copper 1967a). One may suppose (*cf.* Kauffman 1978) that the atrypids were by this way maintaining themselves in somewhat more oxygenated water layers, while toxic conditions were at the sediment/water interface. This could also be an explanation for the underdevelopment of frills (Baliński 1979), while the latter is a typical atrypid adaptation to life on muddy bottom (Ivanova 1962; Copper 1966a, 1967a).

The life position of adult, dorsibiconvex, free-living atrypids is in dispute (Ivanova 1962, Copper 1967a, Bowen & *al.* 1974, Thayer 1974). In the investigated atrypid shell beds, specimens with the flat ventral valve upwards and downwards are equally common (Table 2), and there is no correlation of either position to the shell size (Text-fig. 9C). This is consistent with what was found by Worsley & Broadhurst (1975) in the Silurian atrypids. One may therefore claim that either life position, taken by the adult free-living atrypids, as it is the case with various other extant as well as extinct brachiopods (*see* Makridin 1964, Baliński 1973, Richardson & Watson 1975, Heliasz & Racki 1980), possibly depended upon the substrate nature and microrelief, current activity, frills development and function (*see* Copper 1967a), or even upon population density (*cf.* Mundlos 1978).

The cyrtospiriferids associated with the considered atrypids probably were undergoing a similar ontogenetic changes in the mode of life, as it is evidenced by their delthyrium being gradually covered with delti-

dial plate in ontogeny. The adequate shell orientation seems to have been maintained by free-living individuals due to the balance of their strongly biconvex and posteriorily thickened from (*cf.* Ivanova 1962, Baliński 1973, Fürsich & Hurst 1974, Thayer 1974).

Table 3

Parameter \ Atrypid shell bed		Zamkowa Hill at Chęciny				Dębnik
		F-I		F-II	F-III	
		W	E			
Size of collection		59	77	41	25	117
Shell size (S) [(length + width):2]	S_m	19.5	23.8	24.0	30.9	17.2
	s	4.9	5.3	4.9	4.2	2.7
	C.V.	25.1	22.3	20.4	19.5	15.6
Width index (W.I.) [width/length]	$W.I._m$	1.01	1.04	1.03	1.02	1.03
	s	0.06	0.04	0.07	0.08	0.05
	C.V.	5.9	3.8	6.8	7.8	4.9
Thickness index (T.I.) [thickness/size]	$T.I._m$	0.54	0.60	0.63	0.70	0.58
	s	0.08	0.07	0.10	0.07	0.05
	C.V.	14.8	11.7	15.9	10	8.6
$W.I._m/S_m$ ratio		0.052	0.044	0.043	0.033	0.060
$T.I._m/S_m$ ratio		0.028	0.026	0.026	0.023	0.034

Comparison of atrypid faunas from different shell beds; for explanations see Text-fig. 11
m — medial value, s — standard error, C.V. — coefficient of variability

The atrypids from virtually each of the investigated shell beds from Chęciny show a distinctive external shell morphology (Text-figs 11—12 and 17—19; Table 3). They are nonetheless assigned to a single species, *Desquamatia (Seratrypa) globosa* (Gürich), and interpreted as an expression of purely phenetic variation. The atrypids from Dębnik, however, differ from those found at Chęciny in some characteristics that commonly are recognized (Copper 1966b, 1973) as taxnomically important ones. This difference may actually reflect an ecologically controlled phenetic variation among conspecific but geographically isolated populations, as well as a true interspecific variability (*cf.* Alexander 1977).

SYNECOLOGY OF THE ATRYPID ASSEMBLAGES

Main development of the atrypid shell beds at Chęciny (set F) was confined to a temporary increase in water depth between 2 phases of coral thicket growth. The early stage of development of particular atrypid bed (*cf.* Text-fig 13), however, was related to a considerable increase in environmental energy and a considerable bioclastic influx to the quiet

subtidal habitats. Sometimes, restricted lagoons were reached by turbulent waters which caused, in turn, an abrasion of coral and amphiporoid banks and an influence of brackish (?) water. Under less turbulent conditions calcareous mud was being deposited. The resulting crinoid limestones show some evidence (*e.g.* considerable amounts of pelletal micrite in places, poor sorting, generally disorderly structure and occurrence of swirls) for rather short transportation and intense biogenic reworking, which, was, indeed, suggested for similar deposits by Tyler (1969) and Anderson & Pazdersky (1974). One may therefore suppose that patches of crinoids, tubular algae, corals, and shelly organisms developed during periods with decreased environmental energy.

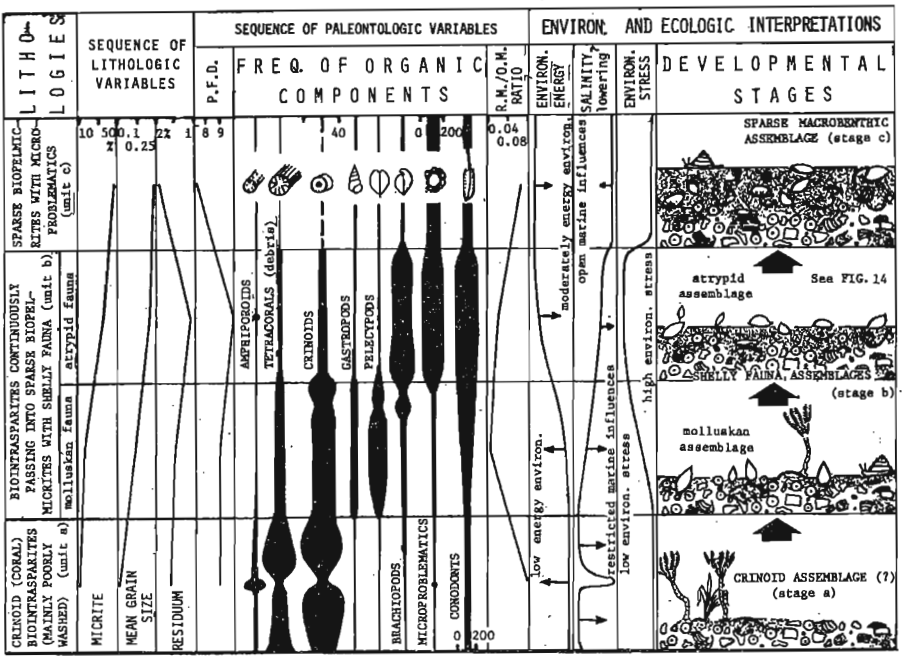


Fig. 13. Developmental pattern of sedimentary cycles of the set *F* of the Chęciny limestones (examplified by the cycle *F-I*); size of arrows indicates the range of variability of environmental factors; the supposed salinity trend is confirmed by geochemical analysis (*see* Racki & Racka 1981); for explanation see Text-fig. 3

Following a further decrease in water turbulence, the unstable crinoidal sands were more densely colonized by shelly fauna. Vagile and eurytopic gastropods seem to have been pioneer forms, succeeded by semi-infaunal end epibyssate pelecypods. The latter may have prevailed over the brachiopods at that stage of the habitat development owing to their greater eurytopy (*see* Bowen & *al.* 1974, Thayer 1974) and greater colonization abillity due to the longer planktic-larval stage (Steele-Petrović 1979). The subsequent explosive colonization by the atrypids may thus

reflect a further stabilization of the environmental conditions and a further stabilization of the environmental conditions and a further decrease in water turbulence and sedimentation rate, as well as changes of substrate. The sharp lower boundary of the atrypid shell beds is suggestive of their development having been related to uncovering of several hard substrates (*e.g.* bioclasts) by a temporary increase in water turbulence (*cf.* Mundlos 1978).

The *Desquamatia globosa* assemblage (Text-fig. 14) is a high-density, low-diversity macrobenthic association strongly dominated by the index species. This indicates preponderance of physical controls on the assem-

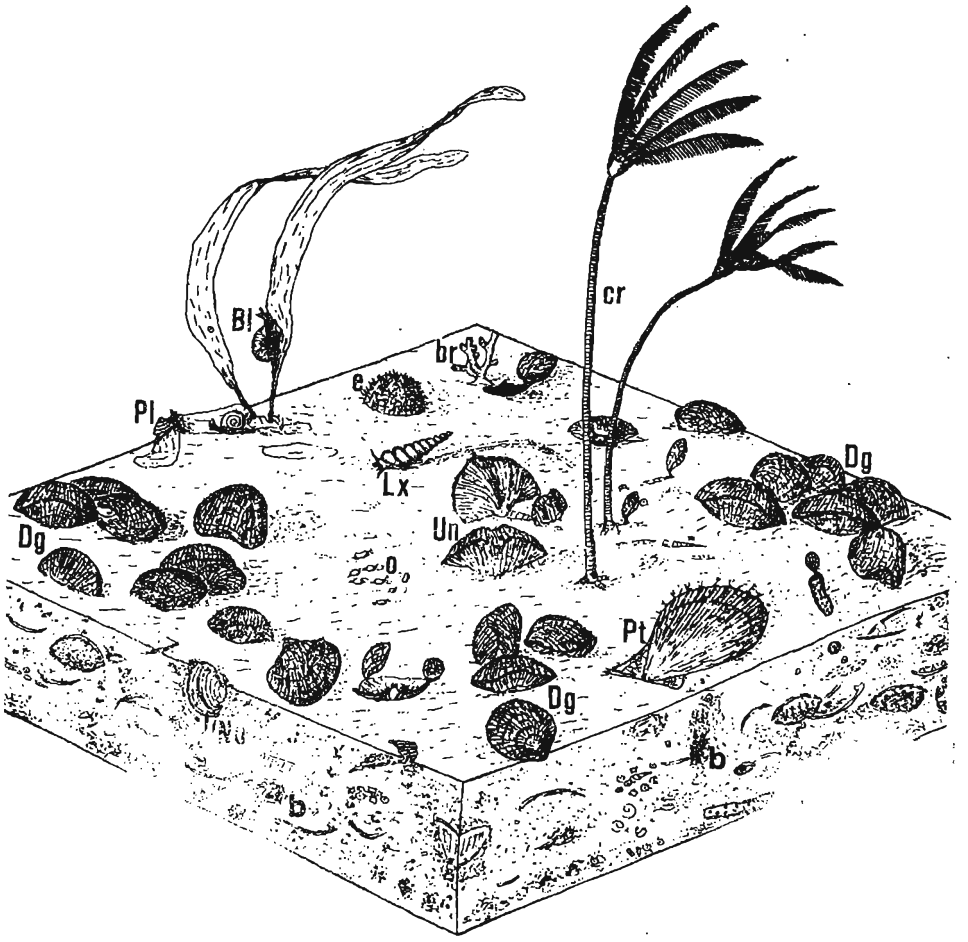


Fig. 14. Idealized bottomscape for the macrobenthic assemblage of the atrypid shell bed *F-I* at Chęciny (drawing by W. Bardziński)
Dg — *Desquamatia (Seratrypa) globosa* (Gürich), **Un** — *Uchtospirifer nalivkini* Lyashenko; **Pt** — pelecypod *Pterinopecten*, **Nu** — pelecypod *Nuculoidea*, **Pl** — gastropod *Pleurotomaria*, **Bl** — gastropod *Bellerophon*, **Lx** — gastropod *Loxonema*, **cr** — crinoids, **e** — echinoids, **br** — bryozoans, **b** — burrows; hypothetical algae at the background

blage and the opportunistic nature of the dominant species (*cf.* Levinton 1970) which is, indeed, typical of pioneer species (Rollins & Donahue 1975, Walker & Alberstadt 1975). The low juvenile mortality suggested by the size-frequency distributions (Text-fig. 11) is notable in this context; in fact, the proportion of juveniles is higher in the shell bed *F-I* than in *F-III*, the latter being deposited under much less turbulent conditions, which indicates that this has not been effected by any post-mortem biases.

The trophic structure of the assemblage was simple, dominated by sessile filter-feeders (brachiopods, crinoids, pelecypods, and possibly bryozoans) which supposedly occupied various microniches different from one another in size and type of the food particles, as well as in feeding level above the sediment/water interface (*cf.* Walker 1972, Boucot 1975, Wallace 1978). In addition, there were some vagile epibenthic grazers and/or detritus-feeders (gastropods and possibly ostracodes and echinoids) and inbenthic detritus-feeders (pelecypods *Nuculoidea* and soft-bodied organisms). The gastropods often occur in nests which may point to the presence in the habitat of some unpreserved benthic algae, their main food resource, although some streamlined bellerophonitids could also be active predators (Linsley 1979). Predators, or any unequivocal evidence for their activity, usually are lacking from Devonian brachiopod assemblages, and this is also the case with the *Desquamatia globosa* assemblage. However, fish may have been feeding upon various larvae (Rudwick 1970) and/or crinoids (Lane 1970).

With the sedimentation rate of modern deposit (Milliman 1974, Wilson 1975) taken into account, the biotope favorable for the atrypids of the shell bed *F-I* persisted over at least a few thousands of years. It finally become extinct due to a gradual environmental evolution toward restricted lagoons, which presumably involved a decrease in salinity and turbulence, an increase in water turbidity, and possibly also a drop in oxygen content of the nearbottom water layers. Most macrobenthic ani-

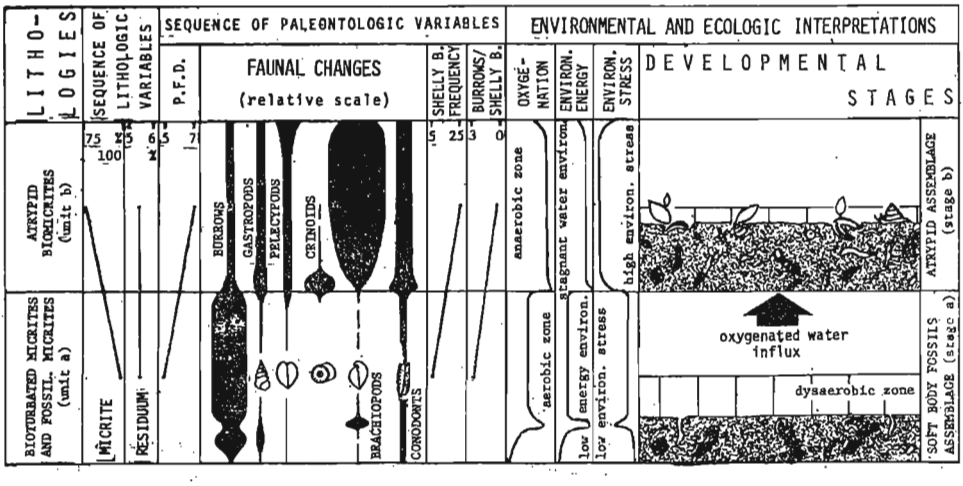


Fig. 15. Developmental pattern for the cycle *II* of the Dębnik limestone; for explanations see Text-fig. 3

mals (except for gastropods) were unable to successfully cope with the new environmental regime, while supposedly planktic microproblematics, as well as ostracodes and infauna flourished.

The main ecological factor controlling the organism distribution at Dębnik was the oxygen content of water. Under stagnant conditions soft bodied inbenthic animals were the only to flourish, temporarily accompanied by some minute gastropods (Text-fig. 15). Periodically, the environment was ameliorated by water exchange, possibly due to storms. Then, shelly animals, mostly vagile benthic ones (gastropods, less commonly echinoids and ostracodes), were rapidly colonizing the biotope. Only rarely the aeration was good enough to permit the preponderance of sessile epibenthic filter-feeders (atrypids, pelecypods, and possibly crinoids). In fact, the epiplanktonic mode of life proposed for various brachiopods found in Dębnik-like environments (*cf.* Thayer 1974, Gratschianova 1979) seems implausible for the atrypids under discussion, if only because of their biostrome-like mode of occurrence.

The recognized pattern of succession of fossil assemblages seems to have been largely controlled by extrinsic, environmental factors. This is evidenced, for instance, by the inhibition of the atrypid assemblage development at an immature stage by an increase in turbulence (bed *F sub-I* at Chęciny) or a decrease in aeration (unit *IIa* at Dębnik). On the other hand, there is no evidence for any biotically controlled changes in the assemblage structure. One may therefore claim that this succession of fossil assemblages is representative of community replacement (Boucot 1975, Hoffman & Narkiewicz 1977; *see also* Ager 1963) rather than true ecological succession (*cf.* Walker & Alberstadt 1975).

SYSTEMATIC DESCRIPTION

Suborder **Atrypidina** Moore, 1952
Superfamily **Atrypacea** Gill, 1871
Family **Atrypidae** Gill, 1871
Subfamily **Atrypinae** Gill, 1871

Genus *DESQUAMATIA* Alekseeva, 1960
Subgenus *SERATRYPA* Copper 1967
Desquamatia (Seratrypa) globosa (Gürich, 1896)

(Text-figs 16—20 and Pl. 8, Figs 1—4, Pl. 9, Figs 2—3, 5—7, and 9—10)

1896. *Atrypa reticularis* Linné var. *globosa*; G. Gürich, pp. 270—271 [*partim*].
Neotype: Specimen No. ZPAL Bp. XXXIV/506, shown in Pl. 8, Fig. 1.
Type horizon: Middle to Upper Devonian boundary.
Type locality: Chęciny, Zamkowa Hill, western quarry, bed *F-I* (Text-figs 2—4).
Material: 63 complete shells, 132 almost complete, and over 400 shell fragments, mostly well preserved.

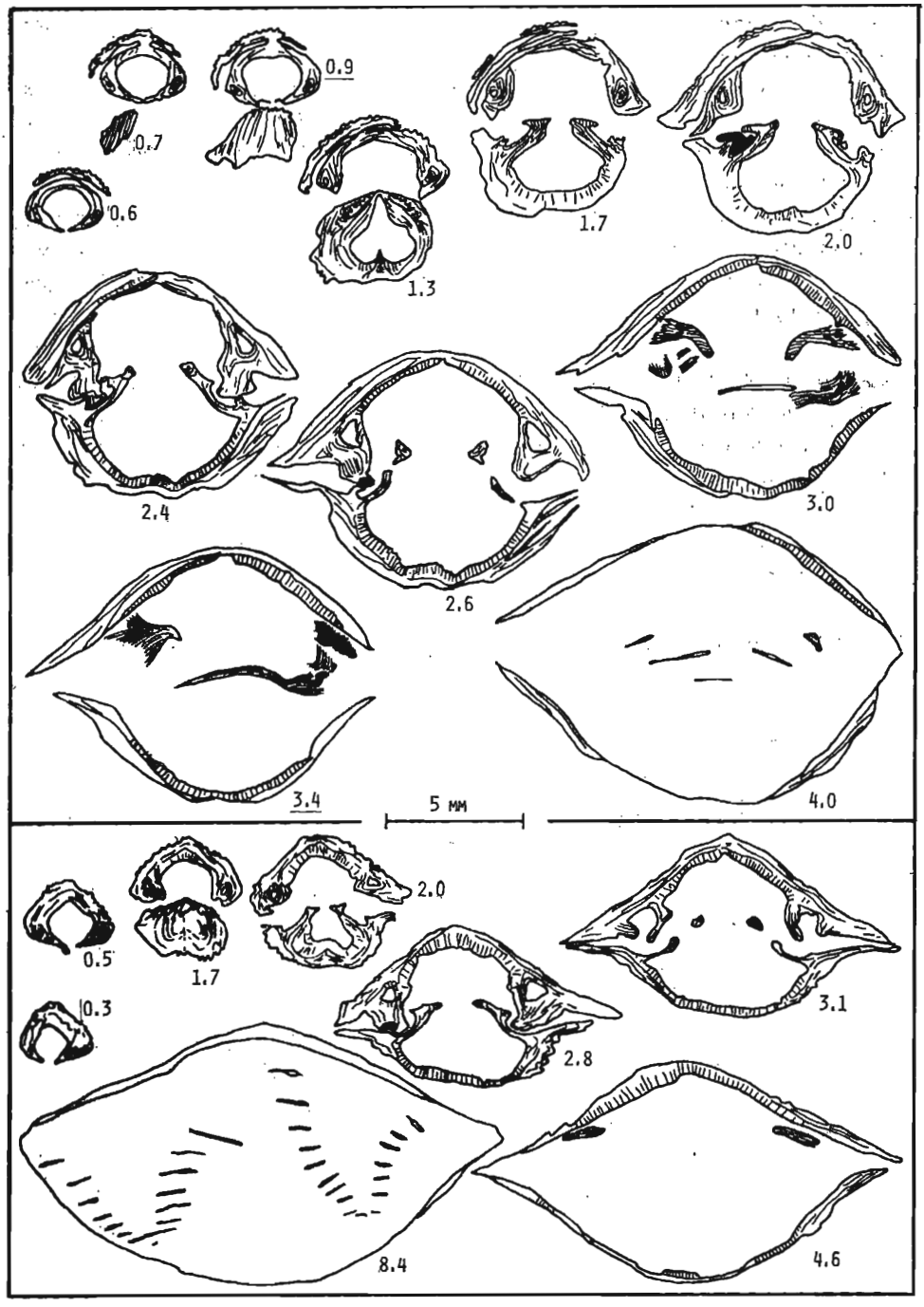


Fig. 16. Transverse serial section of *Desquamatia (Seratrypa) globosa* (Gürich) for two specimens from the shell bed *F-I* (eastern outcrops) at Zamkowa Hill, Chęciny; numbers refer to distance in *mm* from ventral apex

Description. — Shell medium-sized (in the genus), dorsibiconvex to biconvex, subcircular to transverse elliptical in outline, with cardinal margin a little curved, covering some 70% of the shell in width; antero-lateral margins rounded; anterior commissure rectimarginate in juveniles and uniplicate in adults.

Pedicle valve a little convex, with slightly flattened lateral parts in adults; sinus shallow and wide, present in some specimens only; tongue up to 8 mm in length, confined to adults; beak suberect to erect; interareas concave, orthocline to anacline; delthyrium covered with deltidial plates, with elliptic formen in the apical part. Brachial valve strongly convex, with concave postero-lateral parts in adults; fold poorly developed, sometimes with very weak and shallow median furrows.

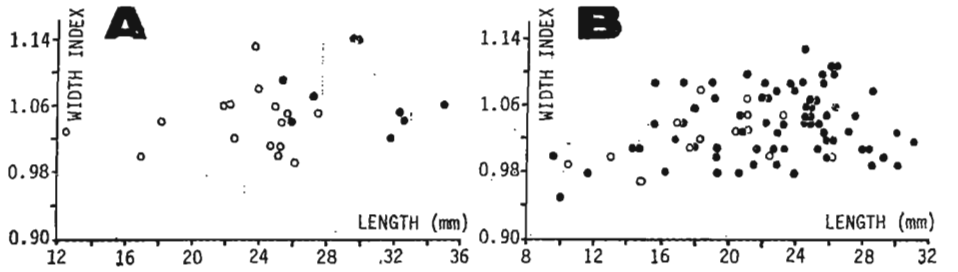


Fig. 17. Dependence of width index to the length of shell for *Desquamatia (Seratrypa) globosa* (Gürich) from Zamkowa Hill at Chęciny
A — specimens from western quarry, beds *F-II* (*circles*) and *F-III* (*dots*); B — specimens from western quarry (*circles*) and eastern outcrops (*dots*), bed *F-I*

Pedicle valve with low (but long dental plates; lateral cavities small; teeth massive, bilobate (Text-fig. 16). Brachial valve with strongly developed hinge plates (Text-fig. 16).

Shell ornamented with fine costae (Pl. 9, Fig. 10), bifurcated at the pedicle valve, intercalated and subordinately bifurcated at the brachial one. Growth lines

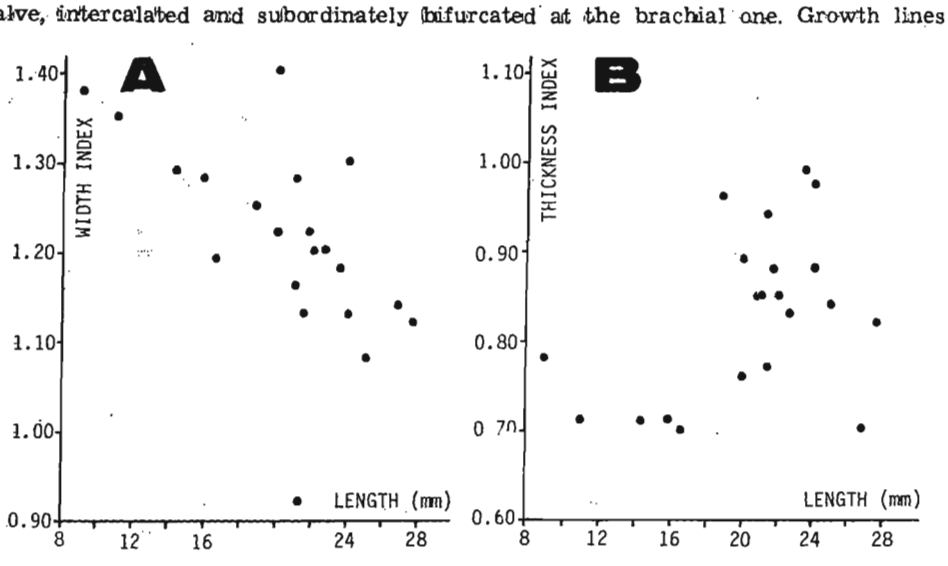


Fig. 18. Dependence of thickness index to the length of shell for *Desquamatia (Seratrypa) globosa* (Gürich); explnations same as for Text-fig. 17

spaced every 2—4 mm, more densely packed anteriorily, inclined. Some specimens preserved with drills (Pl. 8, Fig. 4 and Pl. 9, Fig. 3). Microlines preserved only exceptionally, very weak and densely packed (Pl. 9, Fig. 10).

Variability. — There is much variation in shell width and convexity (Text-figs 17—18 and Table 3). It is notable that small-sized specimens are elongate to isometric in outline, while those exceeding 20 mm in size are much wider than long (Text-fig. 20). There is much variation also in density of costate ornamentation as measured at 20 mm in distance from the umbo (Text-fig. 19). It is notable that stratigraphically older specimens (shell bed *F-I*) usually are more finely ornamented than stratigraphically younger ones (shell bed *F-III*); those derived from intermediate strata (shell bed *F-II*) are intermediate also in their ornamentation (Text-fig. 19C).

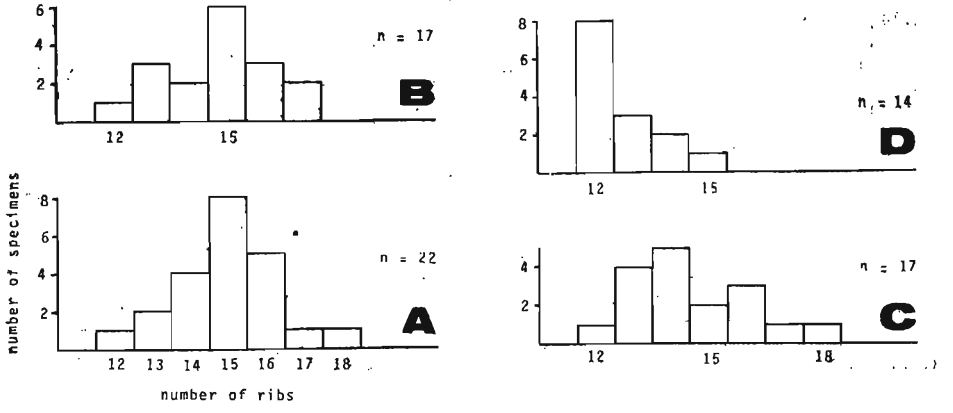


Fig. 19. Variability of rib density for *Desquamatia (Seratrypa) globosa* (Gürich) from the shell bed *F-I* of eastern outcrops (**A**), beds *F-I* (**B**), *F-II* (**C**) and *F-III* (**D**) of western quarry at Chęciny

Remarks. — Gürich (1896) described a number of new varieties of the species *Atrypa reticularis* Linnaeus from the Devonian of the Holy Cross Mts. The variety *globosa* was erected after specimens from Chęciny, Szydłówek, Kadzielnia, Cmentarna Hill (= Kinhofbergen), and Karczówka, but it was not illustrated and any

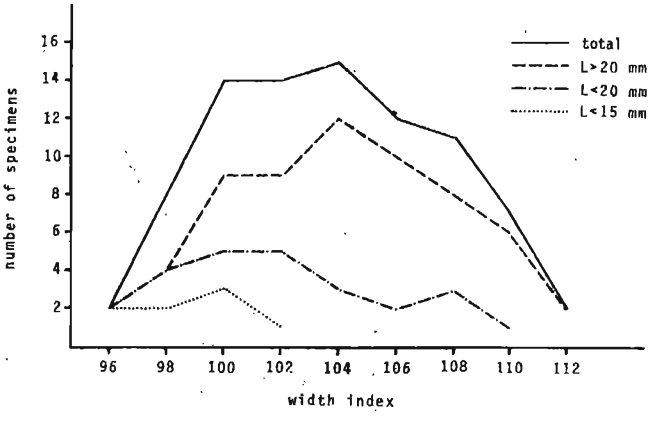


Fig. 20. Variability of width index in different classes of shell size for *Desquamatia (Seratrypa)* globosa (Gürich) from the shell bed *F-I* at Chęciny

pe specimen was not designated. Gürich's collection of *A. reticularis* var. *globosa* entirely lost and therefore, the neotype is here proposed, chosen from the recently discussed large collection from the Zamkowa Hill at Chęciny. At the same time, Gürich's taxon is advanced to the specific rank and called *Desquamatia (Seratrypa) globosa* (Gürich). In fact, specimens from Szydłówek, Kadzielnia, Cmentarna Hill, and Karczówka may belong to another species (one or more). These from the Frasnian *do Iα* of Kadzielnia were, indeed, attributed by Biernat (1971, p. 151, Text-fig. 8 and Pl. 4, Figs 12—13) to the species *Desquamatia (Seratrypa) pectinata* (Schröter, 1777).

The name *Atrypa reticularis* Linn. var. *globosa* was applied by Barrois (1889) for some specimens from the Lower Devonian of Erbray, France, which seem, however, to be not representative of the genus *Desquamatia*; hence, Gürich's name is valid.

The presently discussed specimens of *D. (S.) globosa* very closely resemble *Atrypa reticularis* var. *parazonata* Kelus from the Middle Devonian of Pełcza, Volhynia (Kelus 1939, pp. 18—19, Text-fig. 23 and Pl. 1, Figs 7—9). The only illustrated specimen of the latter taxon differs from *D. (S.) globosa* in having a more rectilinear and long cardinal margin, which causes a posterior displacement of the maximum width of the shell, as well as in its less convex umbonal part of the brachial valve.

The specimens from Chęciny are almost indistinguishable in external morphology from *Atrypa traversensis* Fenton & Fenton from the Givetian Traverse Group, United States (Fenton & Fenton 1930, pp. 6—7, Pl. 2, Figs 12—14). The only difference consists in the ventral sinus being somewhat more sharply defined in some wide specimens of the latter taxon.

The species *D. (S.) globosa* from Chęciny very closely resembles *D. (S.) oneidensis* (Beus) from the Givetian to Frasnian boundary of Dębnik (Baliński 1979). The difference is in that the latter is much smaller-sized (it rarely exceeds 20 mm in length); furthermore, *D. (S.) globosa* shows a less prominent umbo, smaller interareas, and more curved beak at the brachial valve.

The species under discussion resembles also *Atrypa (Desquamatia) zonataeformis* Alekseeva [= *Desquamatia (Independatrypa) zonataeformis*] from the Givetian of the Urals and the Givetian to Frasnian strata of the Kuznetsk basin, Soviet Union (Alekseeva 1962, pp. 73—80, Text-figs 31—35, Pl. 3, Figs 1—5, and Pl. 11, Fig. 1). However, the latter species is larger-sized, more elongate as a rule, and with a longer and more rectilinear cardinal margin (the latter feature is characteristic of the subgenus *Independatrypa*).

Occurrence. — The species *D. (S.) globosa* occurs at the Givetian to Frasnian boundary in the Zamkowa Hill at Chęciny (*see* Text-fig. 2), Holy Cross Mts. It was recorded also at Sosnówka and Zegzelogóra, west of the Zamkowa Hill. Fragmentary specimens possibly attributable to the same species were found in the Jaźwica quarry at Bolechowice and at Sitkówka, Holy Cross Mts.

Desquamatia (Seratrypa) aff. *globosa* (Gürich, 1896)
(Pl. 9, Fig. 4)

***Material*: 3 almost complete shells and some 30 shell fragments.**

Remarks. — The investigated specimens resemble *D. (S.) globosa* from the shell bed *F-I* of the Zamkowa Hill section at Chęciny. On the other hand, the specimens from the shell bed *F-III* which are stratigraphically closer to the form here described are larger and more coarsely ornamented.

Occurrence. — The specimens occur in the upper part of the lithological set *I* in the western quarry and the central pit in the Zamkowa Hill at Chęciny, Holy Cross Mts. (*see* Text-fig. 2).

Desquamatia (Seratrypa) oneidensis (Beus, 1965)
(Pl. 9, Fig. 8)

1965. *Atrypa oneidensis* n. sp.; S. S. Beus, pp. 25—26, Text- fig. 4E—F and Pl. 9, Figs 1—11.
1979. *Desquamatia (Seratrypa) oneidensis* (Beus); A. Baliński, pp. 53—55, Text-figs 18—19 and Pl. 11, Figs 1—9.

Description and discussion. — See Baliński (1979).

Occurrence. — The species occurs in the Hyrum Member of the Jefferson Formation, United States, and at the Givetian to Frasnian boundary at Dębnik, Cracow Upland

Desquamatia sp.
(Pl. 9, Fig. 1)

Material: 2 damaged shells and 2 shell fragments.

Remarks. — The specimens show a weakly convex, almost flat pedicle valve and a strongly convex brachial valve, which makes a difference from much more biconvex *D. (Seratrypa) oneidensis* (Beus) recorded 2.6 m lower in the Dębnik section.

Occurrence. — The specimens were found in the main Carmelite quarry at Dębnik, Cracow Upland, 2,6 m above the shell bed *IIb* (see Text-fig. 6).

Suborder **Spiriferidina** Waagen, 1883
Superfamily **Spiriferacea** King, 1846
Family **Cyrtospiriferidae** Termier & Termier, 1949

Genus *UCHTOSPIRIFER* Lyashenko, 1957

Uchtospirifer nalivkini Lyashenko, 1957
Text-figs 21—22 and Pl. 10, Figs 1—5)

1959. *Uschtospirifer nalivkini* Lyashenko; A. I. Lyashenko, p. 122, Pl. 14, Figs 1—7 [*non* Figs 8—9 = *U. tataricus*].
1973. *Uchtospirifer nalivkini* Lyashenko; A. I. Lyashenko, pp. 88—90, Pl. 27, Figs 1—7 and Pl. 51, Fig. 2.

Material: 20 complete or a little damaged shells and over 70 shell fragments, often distorted and partly scaled off.

Variability. — There is much variation in shell shape and ornamentation. Wide and flat specimens (Pl. 10, Fig. 1) occur with elongate and very convex ones (Pl. 10, Figs 4—5). This dimorphism was interpreted by Lyashenko (1973, pp. 6—8) as a sexual one, but there are also some intermediate forms (Pl. 10, Figs 2—3). There is an ontogenetic increase in shell convexity and elongation (Text-figs 20—21). Rib density ranges from 4.5 to 7 ribs per 5 mm at the anterior margin.

Remarks. — The spiriferid from the Zamkowa Hill at Chęciny has thus far not been described, although it was cited by Sobolev (1909, p. 469) under the name *Spirifer aperturatus (?)* Schloth. Actually, it closely resembles in shell shape and convexity and their variability, as well as in ventral interareas, the species *Uchtospirifer nalivkini* Lyashenko as described from the lowermost Frasnian of northern Timan, Soviet Union (Lyashenko 1959, p. 122). The only difference is in

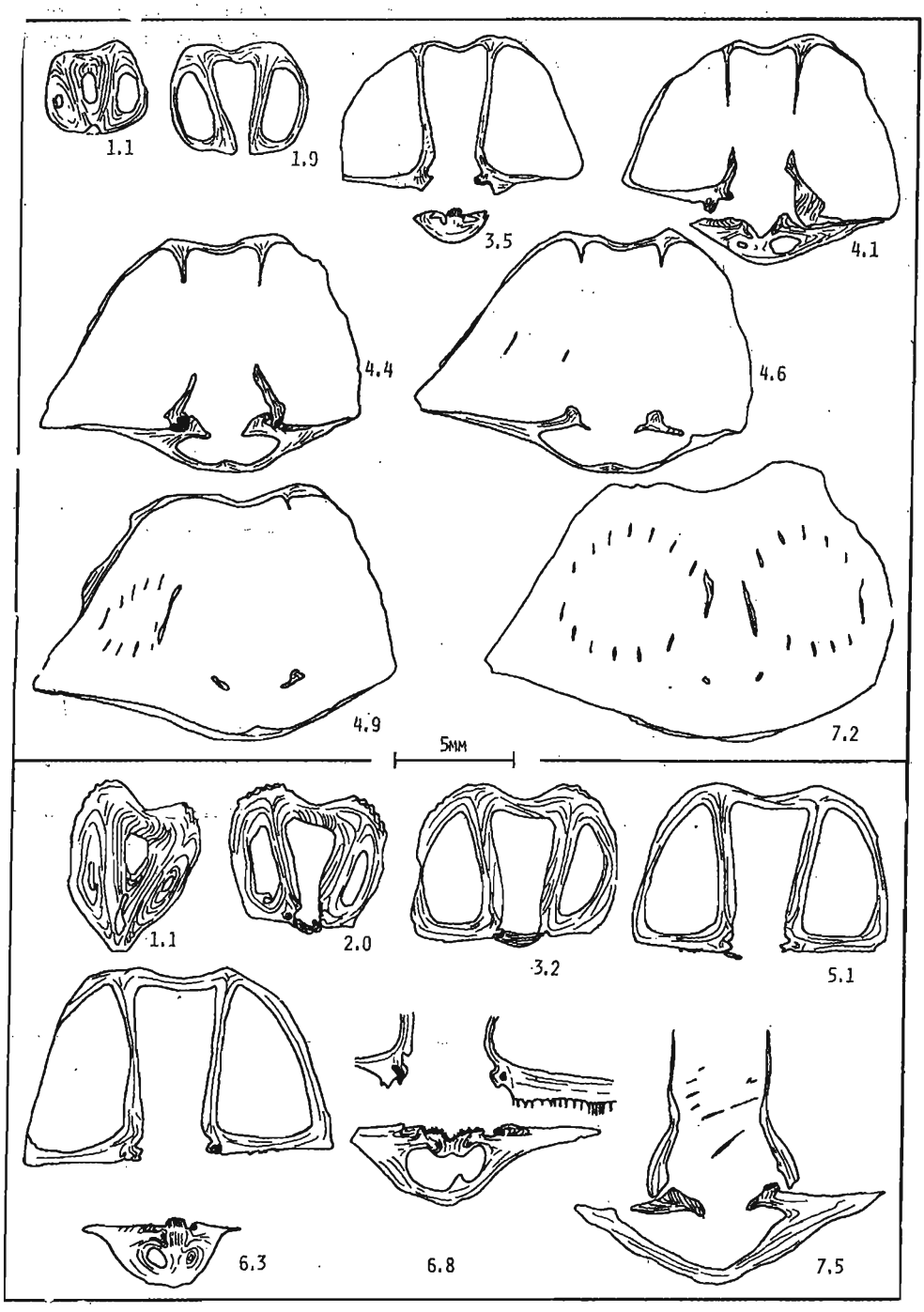


Fig. 21. Transverse serial sections of *Uchtospirifer nalivkini* Lyashenko for two specimens from the shell bed *F-I* (eastern outcrops) at Zamkowa Hill, Chęciny; numbers refer to distance in *mm* from ventral apex

some specimens from Chęciny being more finely ribbed than the type material of the species. Presumably, the specimens from Timan may attain somewhat larger size than the presently investigated ones.

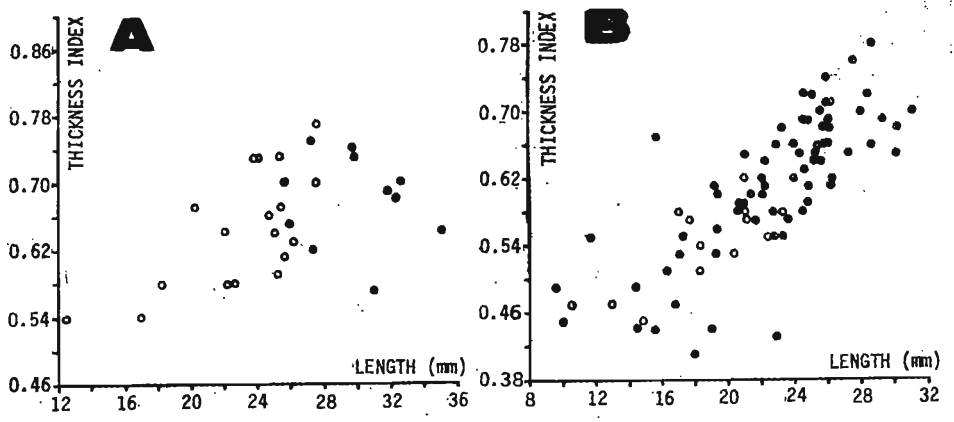


Fig. 22. Dependence of width index (**A**) and thickness index (**B**) to the shell length for *Uchtospirifer nalivkini* Lyashenko from the shell bed *F-I* (eastern outcrops) at Zamkowa Hill, Chęciny

Some specimens from Chęciny resemble also *U. tataricus* Lyashenko from the lowermost Frasnian of the Volgo-Uralian province, Soviet Union (Lyashenko 1969, pp. 46—47, Pl. 9, Fig. 6), but they attain almost twice larger size and a somewhat more finely ribbed than the latter species.

Occurrence. — The species *U. nalivkini* is widespread in the lowe Frasnian of northern Timan, Volgo-Uralian province, and the Urals in the Union. This is its first record in Poland, at the Givetian to Frasnian bound the Zamkowa Hill at Chęciny, Holy Cross Mts (see Text-fig. 2).

Some spiriferid shell fragments found in the Jaźwica Quarry at Bolechow at Jaworznia, at Stopiec (see Gürich 1898, Sobolev 1909), and at the Stokówk Hill, Holy Cross Mts, may also be attributable to the same species.

FINAL REMARKS

All the hitherto recognized monospecific *Desquamatia* shell beds have reported at the Middle to Upper Devonian boundary, presumably within the interval of the Upper varcus to Lower asymmetricus Zone. This holds true for both the investigated and the other shell beds recorded in Poland (*cf.* Sobolev 1909, Biernat & Baliński 1973, Filonowicz 1973), as well as for those in the Rhineland and the Ardennes (Copper 1967b), and United States (Beus 1965, Williams 1973, Johnson 1977). Possibly, the *Desquamatia* assemblages are to be considered as parallel communities (Watkins & *al.* 1973; *cf.* also Wallace 1978) indicative of that stratigraphic interval.

With the *Desquamatia* assemblages compared to their earlier Middle Devonian counterparts, one may claim that *Desquamatia* and/or closely

lated forms (*see* Copper 1973) did occupy at the Middle Devonian ecline several ecological niches realized previously by other atrypid enera, such as *Atrypa* and *Spinatrypa* (*see* Copper 1966a, 1967b); in urn, they were replaced with the rhynchonellids at the younger stratigraphic levels (see Ager & *al.* 1976).

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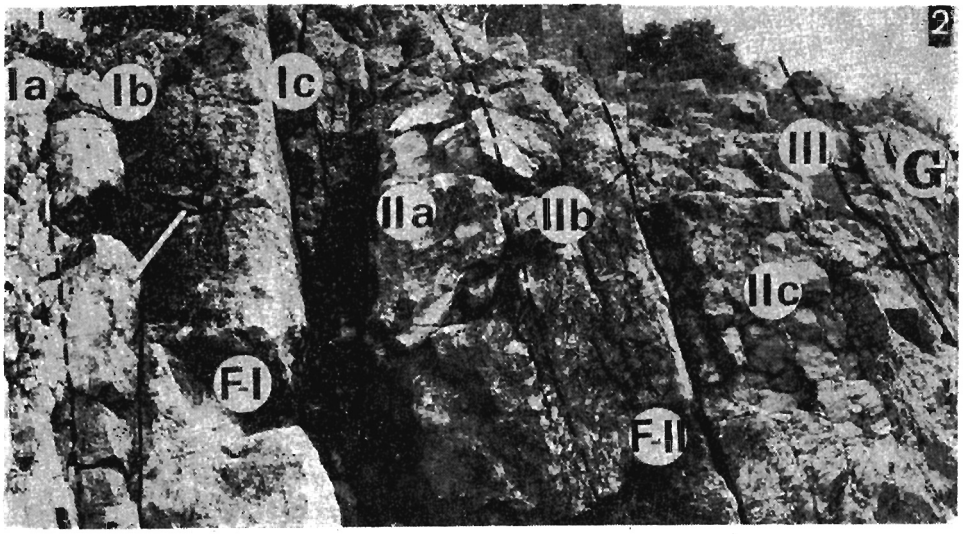
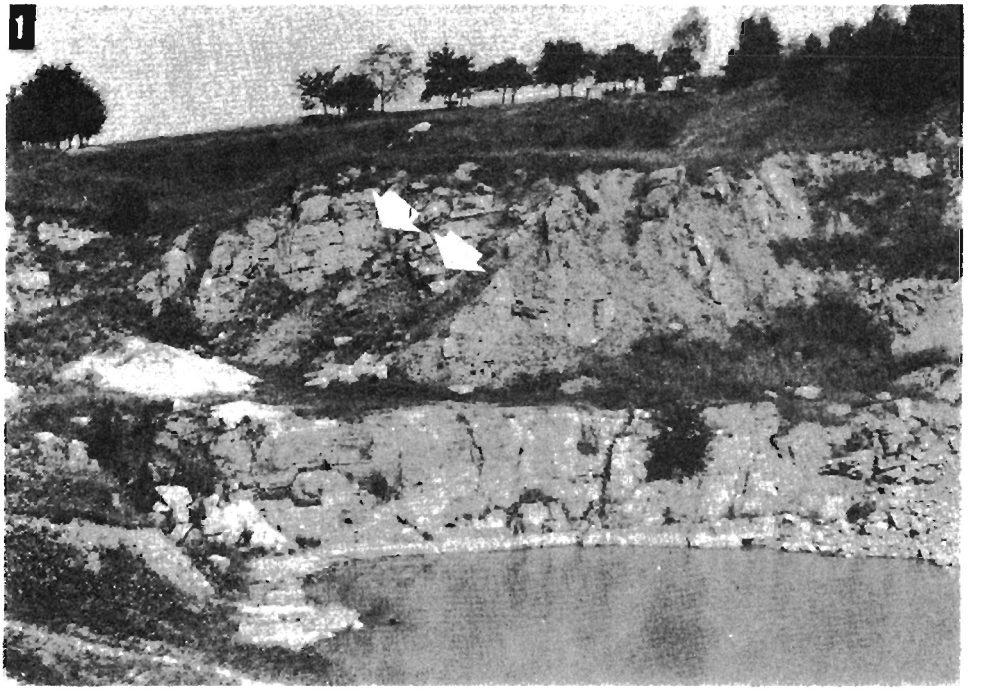
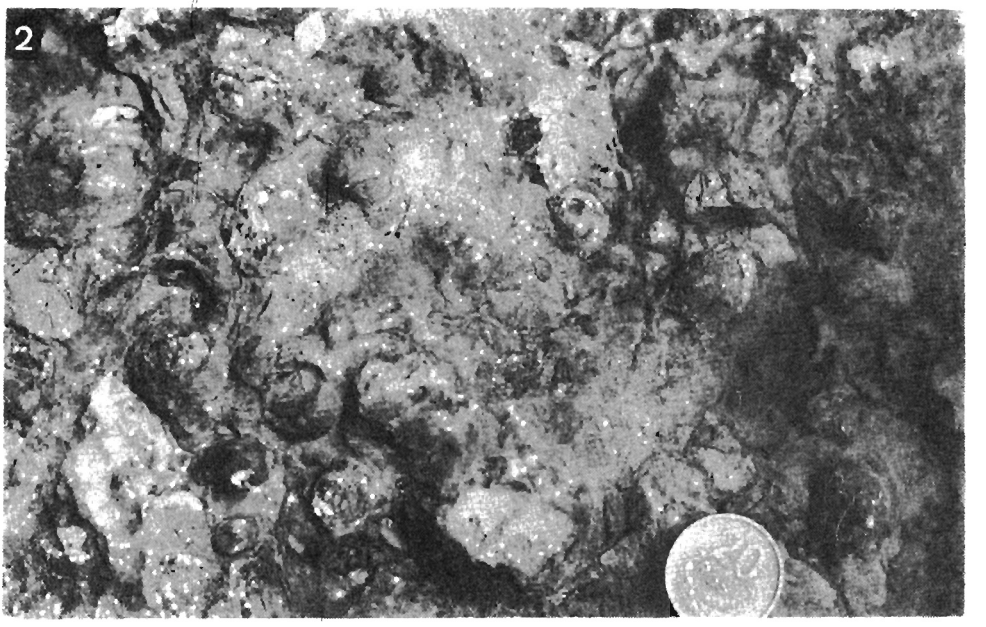


1 — Southern part of the western quarry at Zamkowa Hill, Chęciny, showing positions of atrypid shell beds (*arrowed*); *F-I* lithologic sets (*see* Text-fig. 2)

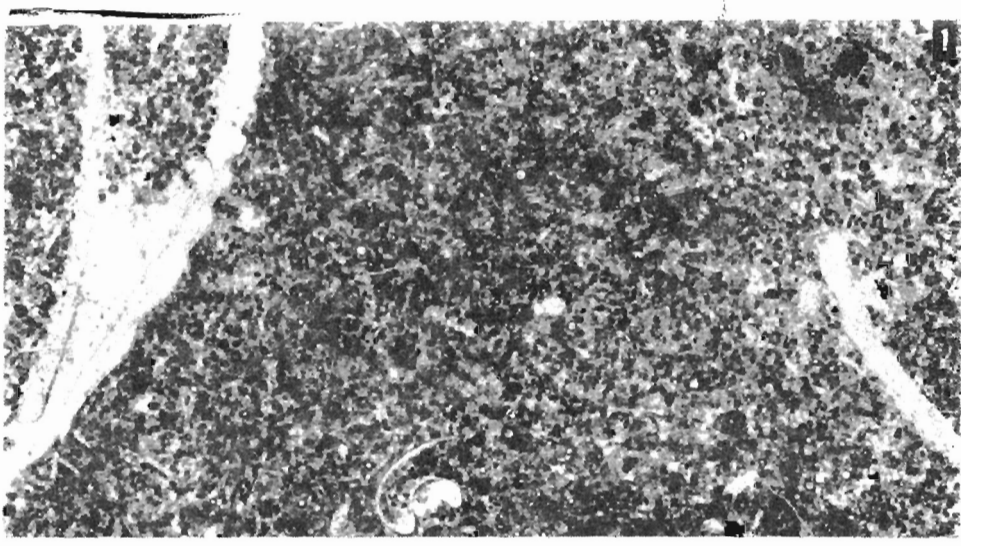
2 — Fragment of the western quarry showing two lower subsets of the set *F* (*F-I* and *F-II*) and passage of the sets *F* and *G*; *I, II, III* smaller lithologic units (*see* Text-fig. 3); Zamkowa Hill, Chęciny

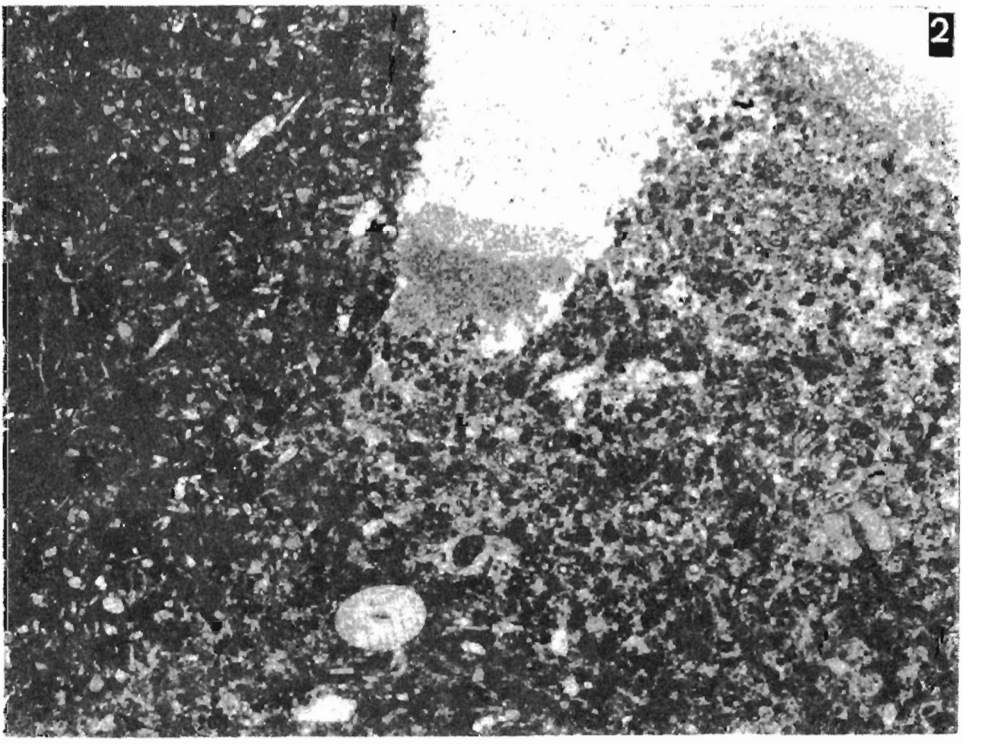


1 — Northern wall of the Main Carmelite Quarry at Dębnik; arrowed are the atrypid beds



2 — Fragment of the top surface of the atrypid bed in the quarry above Rokiczany ravine at Dębnik

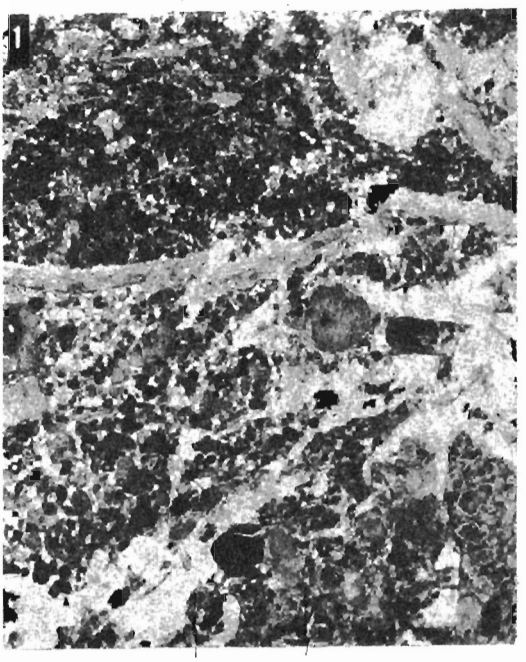


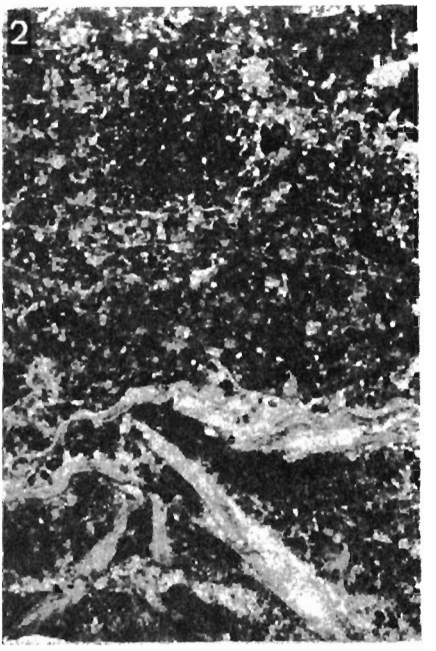


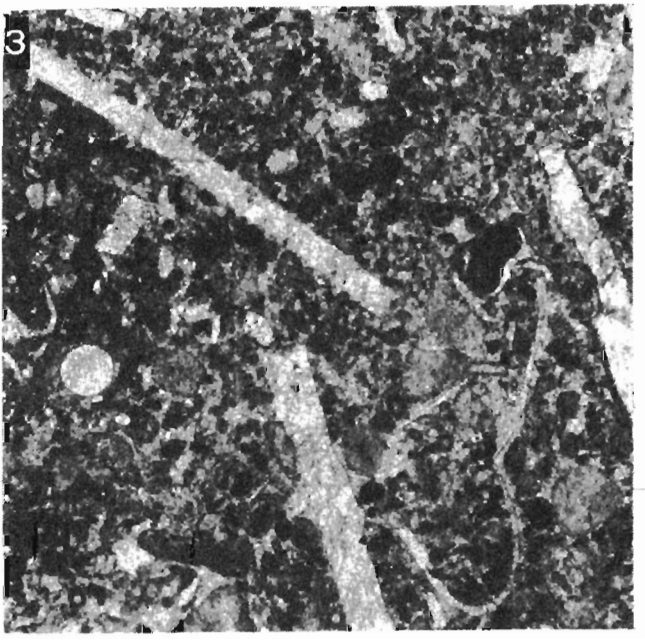
Typical microfacies of the atrypid shell bed *F-I* at Chęciny

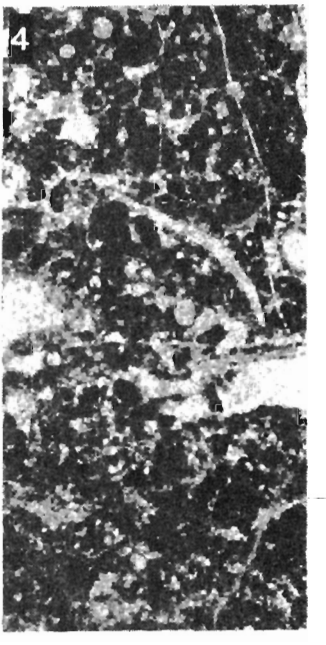
1 — Packed atrypid biopelmicrite (for details *see* Pl. 6, Fig. 4; western quarry; × 10

2 — Structurally differentiated biopelmicrite; part displaying a compactional structure (left, dark side) passes into a cementational structure of the nodule; upper center — geopetal filling of a burrow(?) by non-skeletal mud of two generations; eastern outcrop; × 15









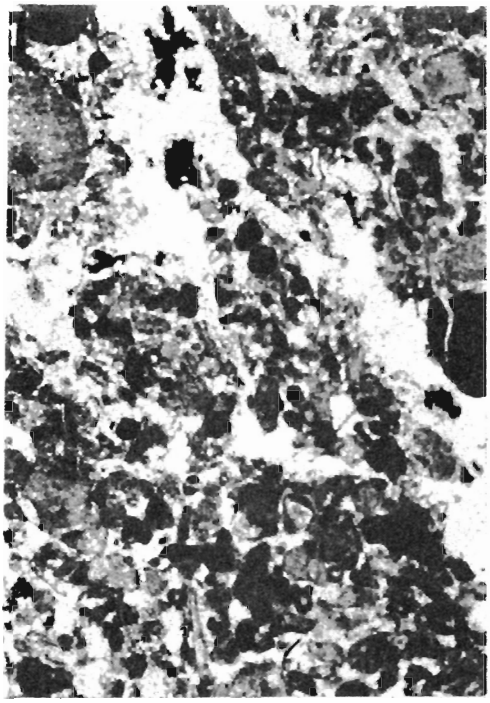
Microfacies associated with the atrypid shell bed *F-I*, western quarry at Chęciny

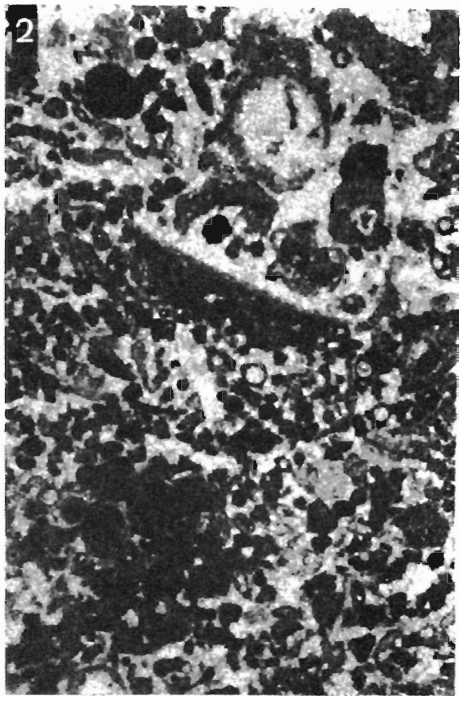
1 — Compactionally squeezed atrypid shell in crinoid-brachiopod biointrasparite; bed *Fsub-I*; × 10

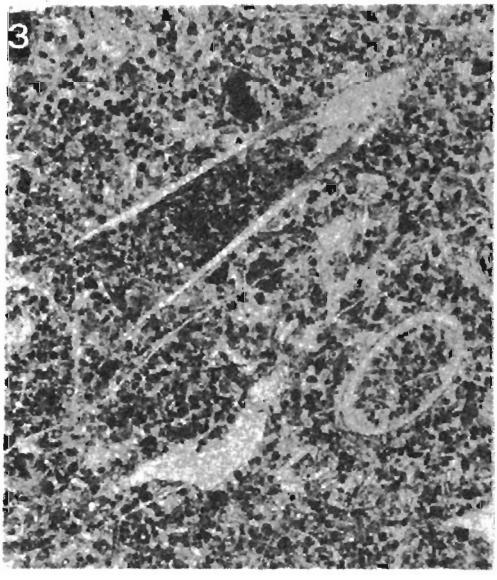
2 — Pressure-welded biopelmicrite (internodular part) showing crushed valves, some with frills; atrypid shell bed *F-I*, level 45 cm; × 15

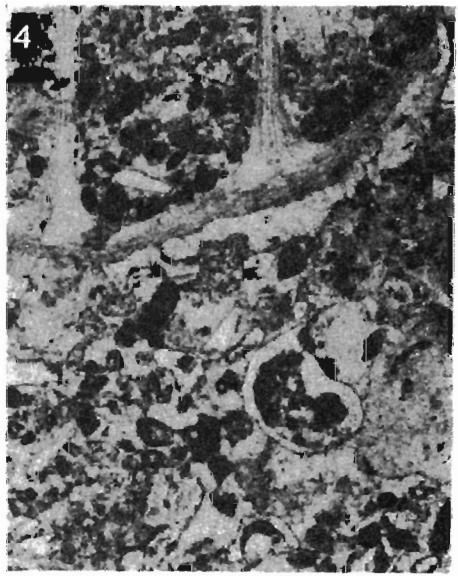
3 — Poorly sorted pelecypod-crinoid biosparite with abundant neomorphic sparite; atrypid shell bed *F-I*, level 5 cm; × 20

4 — Weakly neomorphised biopelmicrite with microproblematics and fragmented valves; unit *F-Ic*; × 25



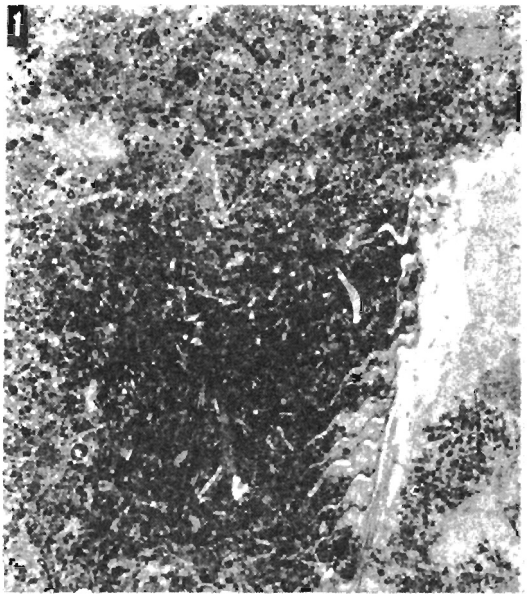


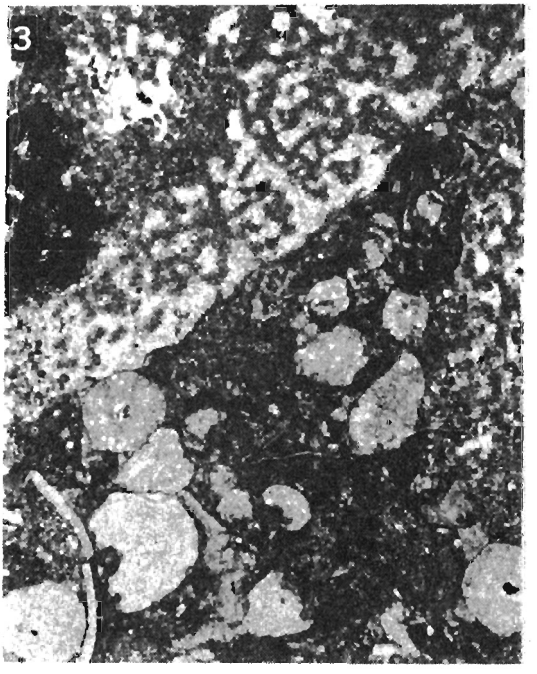


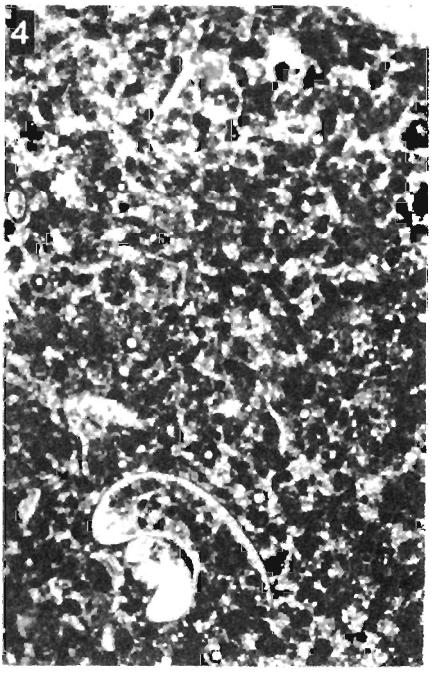


Microfacies associated with atrypid shell beds, western quarry at Chęciny

1 — Poorly-sorted crinoid biointrasparite; bed *Fsub-I*; × 20
2 — Amphiporoid biointrasparite: amphiporoids and micritic intraclasts, some with calcispheres, are visible; in central part, a patch of pelletal micrite below the brachiopod-valve "umbrella"; unit *F-Ia* (middle part); × 20
3 — Neomorphised pelecypod-tentaculitid biopelsparite; set *E*; ×10
4 — Crinoid-pelecypod-brachiopod biointrasparite; note sparry filling below the valve of *Uchtospirifer*, as well as micritic envelopes of many bioclasts; bed *Fsub-I*; × 20







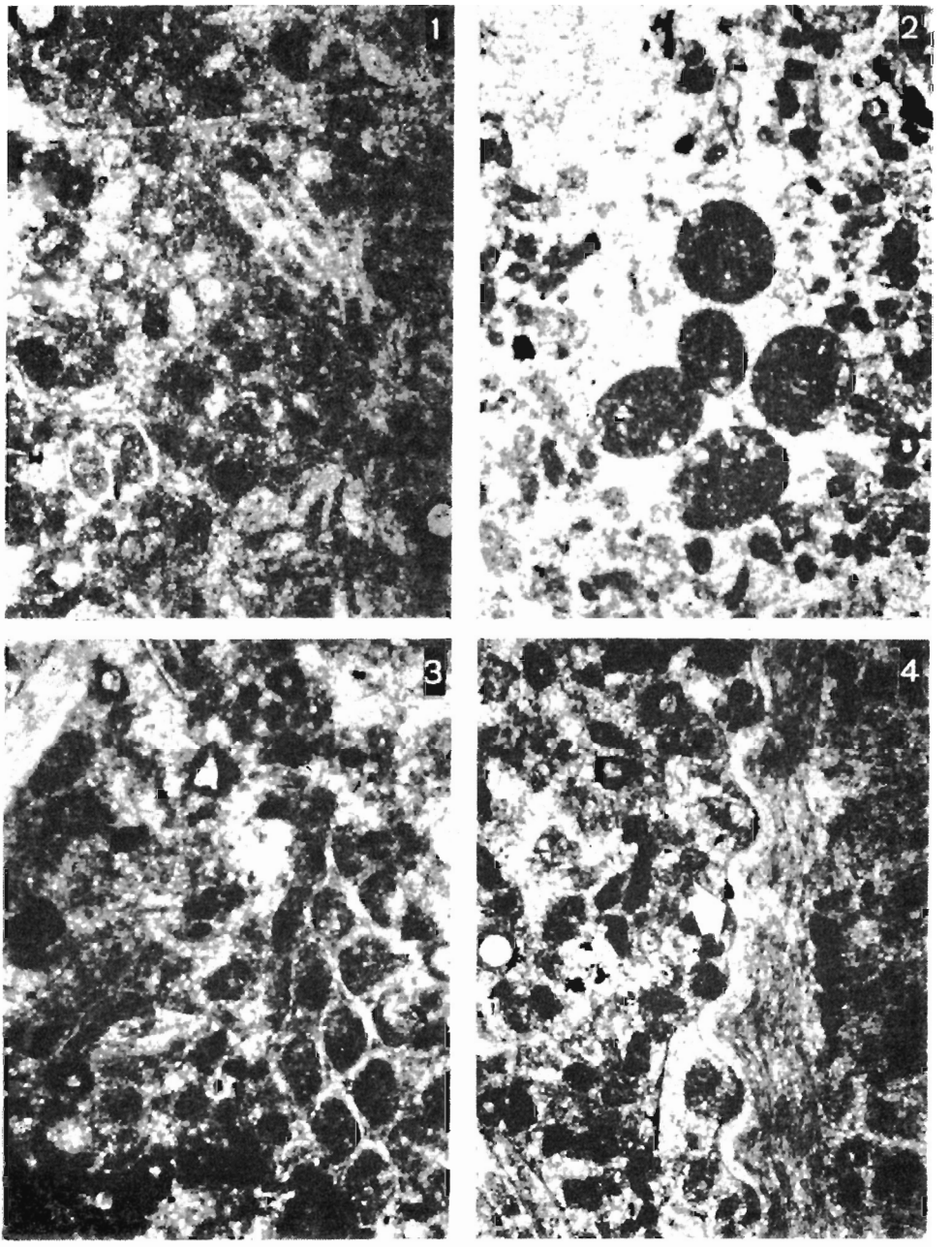
Microfacies of the set *F*, western quarry at Chęciny

1 — Neomorphised, packed atrypid-crinoid biopelmicrite showing variable structure with compacted part at center; atrypid shell with preserved frills is filled by two generations of sediments; atrypid shell bed *F-II*; × 15

2 — Bioturbated, packed biomicrite with mollusks and atrypid fragments, and lamellar *Alveolites*; atrypid shell bed *F-III*; × 15

3 — Strongly deformed crinoid-amphiporoid biomicrite; note numerous pressure-solution contacts of grains; unit *F-IIa*; × 15

4 — Gastropod biopelmicrite; note intraclasts with calcispheres; atrypid shell bed *F-I*, level 20 cm; × 20



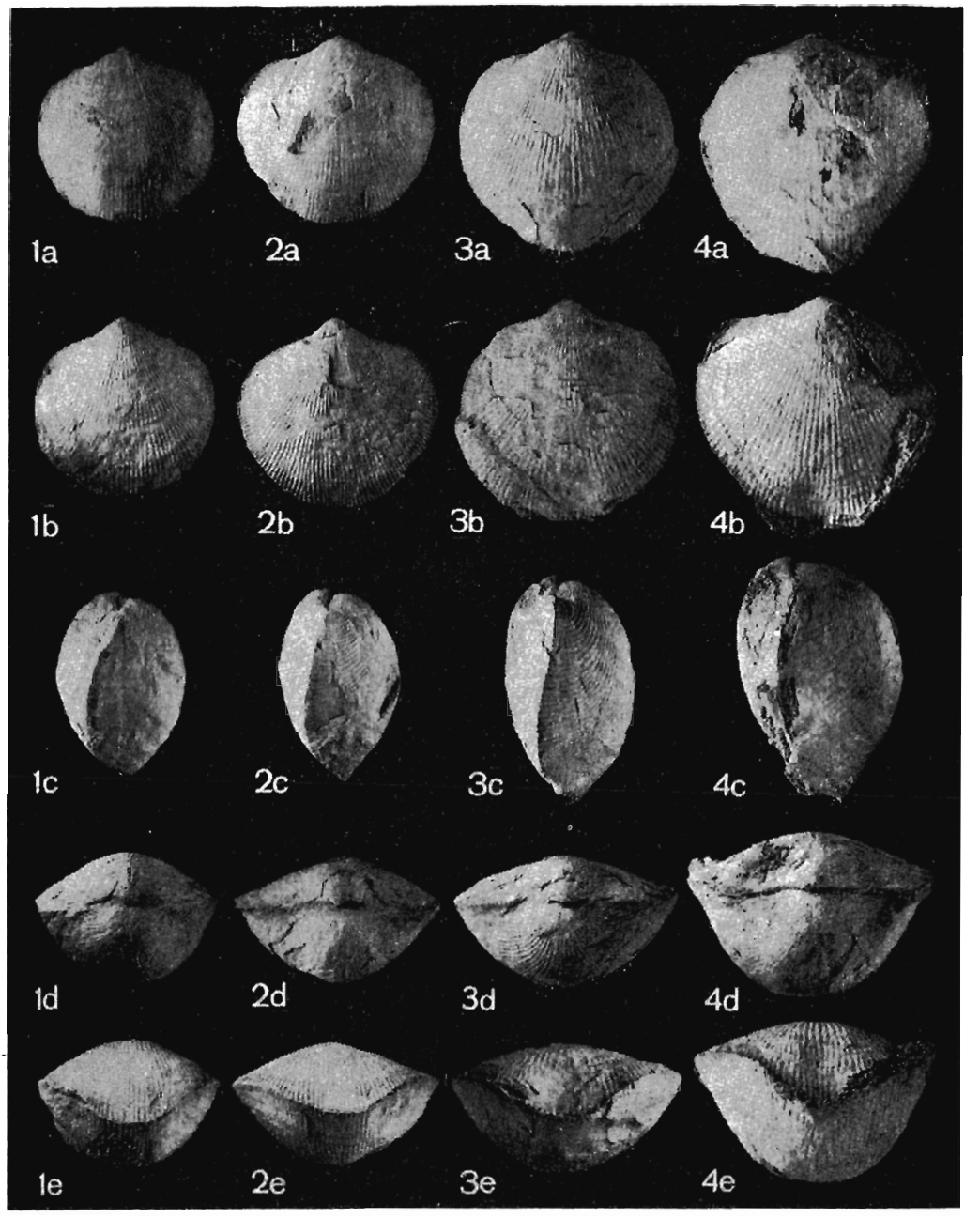
Microfacies of the atrypid shell bed *F-I* at Chęciny

1 — Atrypid biopelmicrite displaying weakly neomorphised matrix and poor assemblages of skeletal grains (microproblematics, ostracodes); western quarry, level 65 cm; × 70

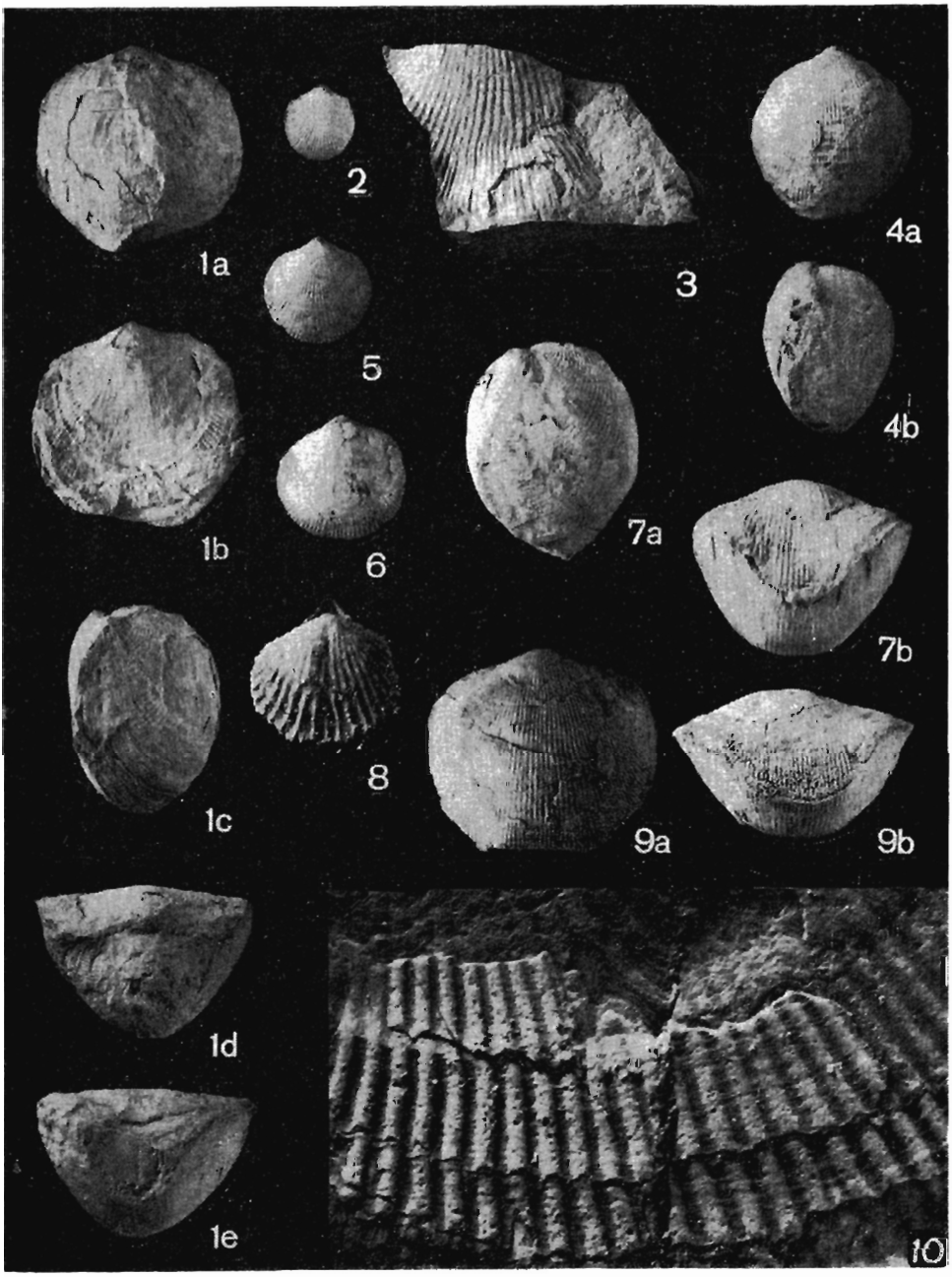
2 — Neomorphised biopelmicrite with a burrow geopetally filled by large pellets; eastern outcrops, level 10 cm; × 35

3 — Biopelmicrite with neosparite and diverse bioclasts (bryozoan zoarium, atrypid valve, microproblematics); western quarry, level 20 cm; × 70

4 — Strongly neomorphised biopelmicrite; note incipient frill of the valve (*arrowed*), synaxial overgrowth on a fragment of the valve, and microproblematics, e.g. *Magnella* (lower left corner); western quarry, level 35 cm; × 70



1—4 — *Desquamatia (Seratrypa) globosa* (Gürich): four specimens in dorsal (*a*), ventral (*b*), lateral (*c*), posterior (*d*), and anterior (*e*) views; Fig. 1 presents the neotype; Chęciny, Zamkowa Hill, western quarry, atrypid shell bed *F-I* (Fig. 1), *F-III* (Figs 3—4), and eastern outcrops, atrypid shell bed *F-I* (Fig. 2); all of nat. size

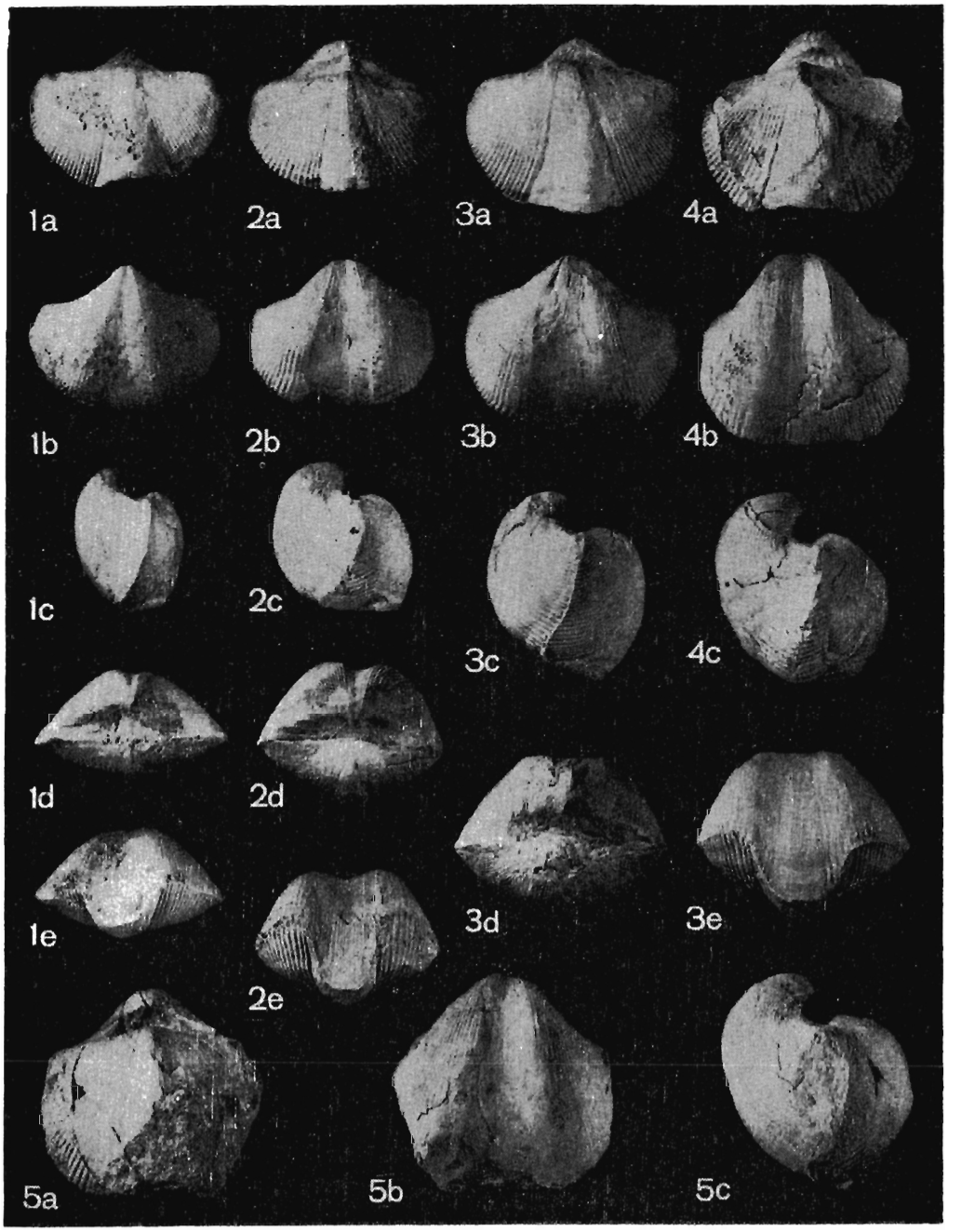


1 — *Desquamatia* sp.: slightly demaged specimen in dorsal (*1a*), ventral (*1b*), lateral (*1c*), posterior (*1d*), and anterior (*1e*) views; Dębnik, Main Carmelite Quarry; nat. size

2—3, 5—7, 9—10 — *Desquamatia (Seratrypa) globosa* (Gürich): 2, 5, 6 — juvenile specimens, 3 — fragment of shell with frills, 7 — strongly convex specimen in lateral (*7a*) and anterior (*7b*) views, 9 — wide specimen in dorsal (*9a*) and anterior (*9b*) view, 10 — microornamentation; Chęciny, Zamkowa Hill, atrypid shell bed *F-I*, eastern outcrops; all of nat. size except of Fig. 10 taken × 8

4 — *Desquamatia (Seratrypa)* aff. *globosa* (Gürich): complete specimen in dorsal (*4a*) and lateral (*4b*) views; Chęciny, Zamkowa Hill, western quarry, atrypid shell bed *F-I*; nat. size

8 — *Desquamatia (Seratrypa) oneidensis* (Beus): juvenile specimen in dorsal view; Dębnik,



1—5 — *Uchtospirifer nalivkini* Lyashenko: 1—3 — variably shaped specimens in dorsal (*a*), ventral (*b*), lateral (*c*), posterior (*d*), and anterior (*e*) views; 4—5 — large specimens in dorsal (*a*), ventral (*b*), and lateral (*c*) views; Chęciny, Zamkowa Hill, atrypid shell bed *F-1*, eastern outcrops; all of nat. size

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G. RACKI i A. BALIŃSKI

INTERPRETACJA ŚRODOWISKOWA DEWOŃSKICH ŁAWIC ATRYPIDOWYCH Z CHĘCIN (GÓRY ŚWIĘTOKRZYSKIE) I DĘBNIKA (WYŻYNA KRAKOWSKA)

(Streszczenie)

Przedmiotem pracy jest analiza ławic z atrypidami *Desquamatia* w stromatoporoidowo-koralowcowych utworach pogranicza dewonu środkowego i górnego Chęcin w Górach Świętokrzyskich i Dębnika na Wyżynie Krakowskiej (*patrz* fig. 1—15, tab. 1—3, oraz pl. 1—7). W obu badanych profilach atrypidy występują w kilku ławicach, które mimo różnego stopnia koncentracji fauny i jej zmienności morfologicznej, charakteryzują się zbliżonymi parametrami tafonomicznymi, typem mikrofacjalnym i zespołem szczątków organicznych. Wszystkie te ławice zajmują zawsze podobną, ściśle określoną pozycję w ukierunkowanej sekwencji zmian lito- i biofacjalnych. Wyraża ona cykliczną zmienność czynników środowiskowych, co doprowadziło do kilkakrotnego zamierania i odradzania się biofacji atrypidowych. Atrypidy wykazywały duże zdolności adaptacyjne, gdyż pionierskie zespoły *Desquamatia* mogły sukcesywnie zasiedlać środowiska śródpłyciznowe zarówno o słabej areacji dna (Dębnik), jak i o zmiennym (?obniżanym) zasoleniu (Chęciny). Duże nagromadzenia muszli tych ramienionogów przyczyniały się do stabilizacji dna przed kolonizacją przez koralowce.

W części systematycznej pracy (*patrz* fig. 16—22 oraz pl. 8—10) opisano atrypidy *Desquamatia (Seratrypa) globosa* (Gürich) i *D. (S.)* aff. *globosa* (Gürich), oraz towarzyszącego im spiriferida *Uchtospirifer nalivkini* Lyashenko.
